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ARTICLE 1

PARALLEL GEOGRAPHIC VARIATION IN THREE *MYIARCHUS* FLYCATCHERS IN THE YUCATÁN PENINSULA AND ADJACENT AREAS (AVES: TYRANNIDAE)

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ABSTRACT

Within the large range of the tyrant flycatcher genus *Myiarchus*, only two islands support three sympatric species—the large, ecologically diverse Jamaica and the small uniform Isla Cozumel, off the Yucatán Peninsula of México. Subspecific separation of the Cozumel and mainland populations has been proposed hitherto only in *M. yucatanensis*, but is described here in *M. tyrannulus* and *M. tuberculifer* as well. New subspecies include a second mainland form of *M. yucatanensis*, the Cozumel form of *tyrannulus*, and the Yucatán mainland form of *M. tuberculifer* (the name currently used for this population was based on a holotype from Cozumel). *M. yucatanensis* is non-migratory. Mexican populations of *M. tyrannulus* are migratory; winter records from the Yucatán mainland may be based in large part on migrants from the north. The species is absent from Isla Cozumel in winter, and the winter range of the Cozumel subspecies is unknown. The Yucatán mainland population of *M. tuberculifer* is non-migratory, but the Cozumel subspecies is absent in winter. Its winter range is unknown, but a migrant has been taken near the coast of eastern Honduras. The character states by which the Isla Cozumel subspecies of all three species of *Myiarchus* are defined are virtually identical, although varying in degree of development. There is no clear trend in characters differentiating other Isla Cozumel endemic subspecies; the factors affecting the parallel evolution of the character states of Cozumel *Myiarchus* are unknown.

INTRODUCTION

Three species of the tyrant flycatcher genus *Myiarchus* (Brown-crested Flycatcher, *M. tyrannulus*; Yucatán Flycatcher, *M. yucata-*

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nensis; Dusky-capped or Olivaceous Flycatcher, *M. tuberculifer*, in decreasing order of size) occur sympatrically on Isla Cozumel, off the east coast of the Yucatán Peninsula of México. The only other island within the range of the genus *Myiarchus* that supports three species is the much larger Jamaica (Lanyon, 1967), where there is altitudinal and ecological separation, at least to some extent, among the species (none of which is conspecific with any of the Cozumel forms). Bond (*in litt.*) believes that, in general, "netting of the 3 species of Jamaica *Myiarchus* in the same place would be very unlikely but not impossible," and, indeed, Lanyon (1967) found all three at Good Hope, where he conducted playback experiments. Isla Cozumel is ecologically relatively uniform (other than disturbed versus undisturbed habitats), and all three of its *Myiarchus* species have been captured in the same mist net lane.

In connection with a field study of the comparative ecology of the three Isla Cozumel species (R. B. Waide, in preparation), large series of specimens were borrowed for measuring. It is likely that no comparable series of *Myiarchus* sp. from the Yucatán area had ever been assembled previously; in addition, the material included a significant number of recently collected specimens in freshly molted plumage, as contrasted to the older, mostly worn spring and summer specimens in most museum series. I therefore examined the specimens assembled for Dr. Waide's interspecific study to see if there is intraspecific variation in the Yucatán area, overlooked by earlier workers because of inadequate material.

The Isla Cozumel population of *Myiarchus yucatanensis* has already been described as *M. y. lanyoni* by Parkes and Phillips (1967). The present study revealed that there is also geographic variation in this species on the mainland of the Yucatán Peninsula, among populations all previously considered *M. y. yucatanensis*. In addition, the Isla Cozumel populations of both *M. tyrannulus* and *M. tuberculifer* are subspecifically separable from those of the mainland, although not as dramatically so as in *M. yucatanensis*. The color differences between island and mainland populations of all three species show remarkable similarities; in other words, the differentiation of the three species has taken parallel routes.

MYIARCHUS YUCATANENSIS

This species is endemic to the Yucatán area, and seems to be a relict form of uncertain relationships within the genus *Myiarchus* (Lanyon, 1965). Neither Lanyon (1965) nor Parkes and Phillips (1967) noted any geographic variation in color within the range attributed to *M. y. yucatanensis* (that is, the peninsular mainland), but when the series

assembled for Dr. Waide's study was arranged geographically, such variation immediately became apparent.

Geographic variation in several species of birds within the Peninsula tends to be correlated with climatic/vegetational zones. Several attempts at classifying such zones were summarized by Paynter (1955:10–15). Details vary, but there is general agreement that rainfall is greatest in the eastern and southern portions (García, 1965) and that vegetation reflects this pattern. Paler subspecies of birds tend to inhabit the more xeric areas to the north, and darker subspecies the more humid areas to the south and east (Paynter, 1955; Parkes, 1974). This pattern is also true of *Myiarchus yucatanensis* on the mainland, and the population of Isla Cozumel, which, with an annual rainfall of 1570 mm, is probably the most humid locality in the peninsular area (Waide, personal communication), is the darkest of all Yucatán Flycatchers and among the darkest of all *Myiarchus*.

The type locality of *Myiarchus yucatanensis* Lawrence is Mérida, in the northern state of Yucatán. The darker form from the humid area of the peninsula thus requires a name. It may be called:

Myiarchus yucatanensis navai, new subspecies

Holotype.—CM 142205, adult female from 8 km NNE of Chetumal, Quintana Roo, México, collected by Santos Farfán B. and prepared by Juan Nava S. for Kenneth C. Parkes, on 1 February 1965 (field no. KCP 2332).

Characters.—To some extent intermediate in color between *M. y. yucatanensis* and *M. y. lanyoni*. The throat and breast of *navai* are slightly darker gray than in *yucatanensis* but not as dark as in *lanyoni*, and the lower breast lacks the olivaceous tinge of *lanyoni*, being, if anything, slightly washed with brownish. The gray of the anterior underparts extends farther posteriorly than in *yucatanensis* and the gray of the sides and flanks restricts the extent of the yellow of the abdomen, as in *lanyoni* but somewhat less extensively (in well made skins of *yucatanensis*—not understuffed so that the sides are pulled together toward the middle—the gray of the sides hardly shows beyond the folded wings, whereas in *navai* and even more in *lanyoni*, the gray of the sides extends medially). The sides and flanks are a clearer, less greenish gray than those of *lanyoni*. The abdomen color, season for season (this area fades rapidly—see Parkes and Phillips, 1967, for details), is paler than in *yucatanensis* and not noticeably different from that of *lanyoni*.

Dorsally *navai* is darker than *yucatanensis*, but freshly molted birds lack the blackish cast of *lanyoni*. The back of *navai* is browner, less greenish than in *yucatanensis*, and thus contrasts less with the brown

of the crown, which is distinctly darker, more chocolate and less reddish brown than in the nominate race.

The effect of dorsal fading with season is shown by the fact that two 20 April skins of *lanyoni* are scarcely darker above than September and October specimens of *navai*. The April *navai* are immediately identifiable as such, however, by the relative extent of the yellow abdominal area. Similarly, the distinction between *navai* and *yucatanensis* in dorsal coloration is much less obvious in worn and faded specimens.

Range.—Southern Quintana Roo and southeastern Campeche, México, northern Petén (Guatemala), and probably northern Belize (Russell, 1964). For a discussion of intergradation with nominate *yucatanensis*, see *Remarks*, below.

Etymology.—It is a pleasure to dedicate this new subspecies to Sr. Juan Nava Solorio, now of Bacalar, Quintana Roo, México, who accompanied me during most of my Mexican field work, and whose indefatigable persistence on Isla Cozumel provided the holotype of *Myiarchus yucatanensis lanyoni*.

Remarks.—Only two specimens from southeastern Campeche have been examined—28 km N (CM) and 8 km W (UW) of Xpujil. Unfortunately, the first of these is a “dilute” freak as far as its brown pigments are concerned. The other is a badly shot specimen in very heavy first prebasic molt. However, the extreme amount of gray and the reduction of yellow on the underparts of the CM specimen, and the darkness of the new dorsal feathers of the UW specimen, indicate that the SE Campeche population is, not surprisingly, assignable to the race of adjacent southern Quintana Roo.

Specimens from western and southwestern Campeche are nearest *navai* but variably intermediate toward *yucatanensis* in dorsal color. Ventrally, the throats of these birds are as pale gray as in *yucatanensis*, but abdomen color in seasonally comparable specimens is nearer *navai*. The extent of gray on the sides and flanks is intermediate between the two races.

Three specimens (USNM) from coastal northeastern Quintana Roo (Puerto Morelos, 2; La Vega, 1) are unfortunately old (1901) and seasonally rather faded (March). However, the color of the underparts clearly matches *navai*. The two Puerto Morelos specimens are not separable from March *yucatanensis* dorsally, but the La Vega specimen is fully as dark as comparable material of *navai*. Two specimens from Tabi (Taabi), central Quintana Roo (YPM, MCZ) resemble the Puerto Morelos specimens in matching *navai* ventrally and *yucatanensis* dorsally.

The Yucatán Flycatcher is known from northern Belize only from sight (and sound) records (Russell, 1964). Occurrence in this area

would be expected, and this population is undoubtedly referable to *navai*.

Specimens examined.—*M. y. yucatanensis*: MÉXICO: Yucatán: Chemax, 1; Chichén Itzá, 21; Progreso (14½ km S), 2; Temax, 1; Tunkas, 1; Xocempich, 3; unspecified, 7. *M. y. yucatanensis* × *navai*: MÉXICO: Quintana Roo: Puerto Morelos, 2; Tabi, 2. Campeche: Champotón and vicinity, 6; Ichek, 1; Matamoros, 1; Pacaitun, 2. *M. y. navai*: MÉXICO: Quintana Roo: Chetumal and vicinity, 3; La Vega, 1. Campeche: Xpujil (8 km W), 1; Xpujil (28 km N), 1. GUATEMALA: Petén: Tikal, 1. *M. y. lanyoni*: MÉXICO: Quintana Roo: Isla Cozumel (various localities), 11.

MYIARCHUS TYRANNULUS

Of this, the largest of the *Myiarchus* flycatchers of the Yucatán area, all of the Mexican populations of the Caribbean slope from the lower Rio Grande through the Yucatán Peninsula (including Isla Cozumel), and those of Belize, eastern Guatemala, and mainland Honduras, have been assigned to *M. t. cooperi* Baird, the holotype of which is a Verreaux specimen from "Mexico" (Deignan, 1949). Paynter (1955:194) stated that this species is found "throughout the [Yucatán] Peninsula, including Isla Cozumel, during all seasons." As the northern populations of this subspecies are known to be migratory, it is difficult to be certain of the status of the winter records from the mainland of the Yucatán Peninsula. Paynter's inclusion of Isla Cozumel in his statement of presence "during all seasons" is puzzling. I have seen no winter specimens, and we failed to find the species on Cozumel during a thorough search in two and a half weeks of November 1965, nor had we found it during an earlier visit 20–23 January 1965. Bond (1961) observed *Myiarchus tyrannulus* on Isla Cozumel in mid-February 1961, and Waide (personal communication) did not see it before 1 March in 1979. The return of the first migrants to the island is thus presumably between late January and early March, unless Bond's birds were wintering stragglers from the north. According to unpublished observations made in 1977, 1978, and 1979 by Barbara MacKinnon de Montes, this species was seen on Isla Cancún (ca. 50 km N of Isla Cozumel) only between 2 April and 21 August. In Gallon Jug, northwestern Belize, E. O. Willis was in residence from 15 February to 1 August 1957, but saw *Myiarchus tyrannulus* only from March through July, and S. M. Russell saw obvious northbound migrants on Calabash Cay, off Belize, on 9 and 10 April 1956 (Russell, 1964). It thus appears certain that the insular populations of this species in the Yucatán area are migratory. In addition, many of the midwinter records of this species on the Yucatán Peninsula may pertain to individuals originating farther north. Unfortunately this cannot be documented through geographic variation, as I have been unable to distinguish among specimens from the various parts of the generally

accepted range of *M. t. cooperi*, with the sole exception of those from Isla Cozumel. If some or all of the Yucatán Peninsula population of *Myiarchus tyrannulus* does, indeed, depart in the late summer or fall (as appears to be true of the populations of Islas Cozumel and Cancún and of northern Belize), it is replaced by wintering birds taxonomically indistinguishable from the breeding population.

Lanyon (1960) stated that *Myiarchus tyrannulus* had not differentiated on Isla Cozumel, but did not indicate the extent of his comparative series. He recognized *M. t. insularum* Bond of the Honduras Bay Islands, which is *less* strongly differentiated from *cooperi* than is the undescribed Isla Cozumel population, which may be called:

Myiarchus tyrannulus cozumelae, new subspecies

Holotype.—CM 143356, adult male from Cedral, Isla Cozumel, Quintana Roo, México, collected by Juan Nava S. for Kenneth C. Parkes, on 19 April 1968 (field no. KCP 3064).

Characters.—Similar to *M. t. cooperi* of the adjacent mainland (and elsewhere) in size, but distinctly darker and browner, less greenish above, with (especially) crown and upper tail coverts darker, richer brown; rufous inner margins of rectrices darker; gray of upper breast tending to invade yellow of lower breast; posterior underparts in general slightly paler yellow; axillars distinctly more whitish, less yellow (in *extremely* worn and faded specimens, the axillar color and the extent of gray on the chest may be the only reliable characters). Nearer *M. t. insularum* of the Bay Islands of Honduras in dorsal color, but even darker than that race; otherwise differs from *insularum* as from *cooperi*. Bond (1936) described *insularum* as having underparts averaging slightly darker than in *cooperi*, but he had only three specimens of the former (and an unspecified number of the latter). The much larger CM series shows that *insularum* does not differ from *cooperi* in either the gray of the throat and breast or the yellow of the abdomen. The subspecies *insularum* is, in fact, intermediate between *cooperi* and *cozumelae* in color, matching the former in ventral color and approaching the latter in dorsal color.

Range.—Known to breed only on Isla Cozumel, Quintana Roo, off the east coast of the Yucatán Peninsula, México; Isla Cancún specimens should be examined. Winter range unknown.

Etymology.—Named for the island it inhabits.

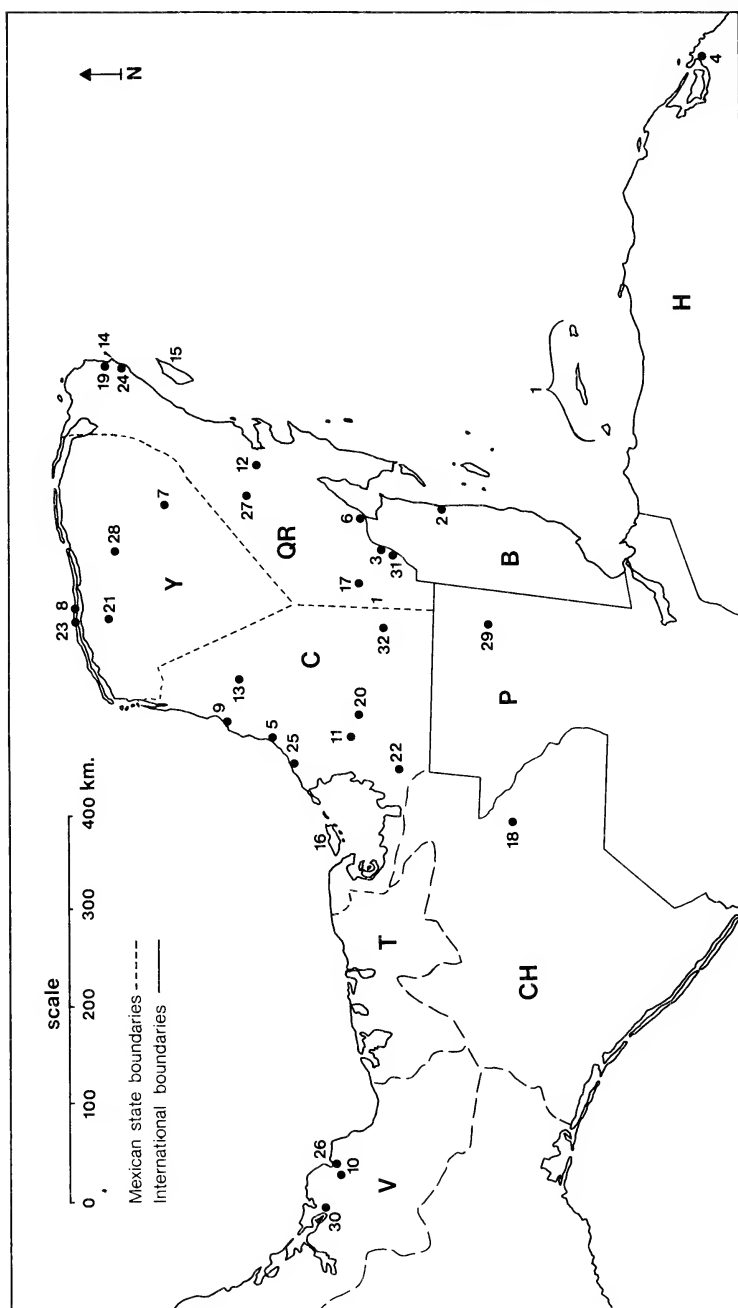
Remarks.—Although the color differentiation of the Isla Cozumel population of *Myiarchus tyrannulus* is much less striking than that of *M. yucatanensis*, some interesting parallel tendencies may be noted. Although *M. t. cozumelae* does not approach the dorsal blackness of *M. y. lanyoni*, nevertheless it is both darker and browner than its

mainland relative. Both *cozumelae* and *lanyoni* share the invasion of gray into the yellow of the posterior underparts, although in *cozumelae* this invasion does not extend as far posteriorly along the sides as in *lanyoni*. Both of the Cozumel races have whitish rather than yellow axillars. Finally, although differences in the yellow of the underparts were not mentioned in the original description of *M. y. lanyoni* (Parkes and Phillips, 1967), the addition of the fresh-plumaged series taken by Waide shows that in *lanyoni* the yellow is noticeably paler than that of the mainland nominate race, just as is true of *M. t. cozumelae* versus *M. t. cooperi*. There is no character in which *M. t. cozumelae* differs from *M. t. cooperi* that is not similarly or more strongly differentiated in *M. y. lanyoni* as compared with *M. y. yucatanensis*.

Specimens examined.—*M. t. cooperi*: TEXAS: Brownsville, 2; Cameron Co. unspecified, 2. MÉXICO: Tamaulipas: Alta Mira, 3. Veracruz: Catemaco and vicinity, 3. Chiapas: Mapastepec (10 km N), 1. Yucatán: Chichén Itzá, 6; Chicxulub Puerto, 1; Dzidzantún, 1; Mérida, 1; Progreso (9–14 km S), 3; San Felipe, 1; Santa Clara, 1; Temax, 1; Xbec, 1; unspecified, 2. Quintana Roo: Chetumal, 6; La Vega, 1; Tabi, 1. Campeche: Champotón, 2; Isla del Carmen, 4. BELIZE: various localities, 10. HONDURAS: various mainland localities, 19. *M. t. insularum*: HONDURAS: Bay Islands (various), 22. *M. t. cozumelae*: MÉXICO: Quintana Roo: Isla Cozumel (various localities), 11.

MYIARCHUS TUBERCULIFER

This is the smallest and most abundant of the *Myiarchus* flycatchers in the Yucatán Peninsula and adjacent areas. The species as a whole, like *M. tyrannulus*, is found from the southwestern United States to Argentina and Brazil, but it has been much more plastic than *tyrannulus*. Traylor (1979) admitted twelve subspecies of *tuberculifer* and only six of *tyrannulus*. Within the area occupied by the two northern subspecies *M. tyrannulus magister* (Pacific) and *M. tyrannulus cooperi* (Caribbean), five subspecies of *M. tuberculifer* were admitted by Traylor. This contrast in plasticity may well be associated with increased opportunity for gene flow in the strongly migratory *tyrannulus*; only the northwesternmost subspecies of *tuberculifer*, *M. t. olivascens*, has been considered migratory. In such a plastic species as *Myiarchus tuberculifer*, it is hardly surprising to find that the Isla Cozumel population, contrary to current usage, is subspecifically separable from that of the adjacent Yucatán Peninsula mainland. What is surprising is that the Isla Cozumel population is migratory, whereas that of the mainland is not. In January 1965 we failed to find *M. tuberculifer* on Cozumel, although it was singing abundantly on the mainland, separated only by a 20 km channel. Two and a half weeks of searching for *Myiarchus* on the island in November of the same year yielded only *M. yucatanensis lanyoni*. As we could not believe that the species had become extinct on the island (it had been collected as recently as 8



August 1962; KU 40675), the only viable alternative theory was that, for some unknown reason, *Myiarchus tuberculifer* is migratory on Isla Cozumel. Such proved to be the case; the species was abundant on the island on 19–20 April 1968, in areas from which it had been absent during our January and November visits. The factors underlying this difference between the Cozumel and mainland populations will be discussed by Waide (in preparation).

The name *platyrhynchus* Ridgway is currently used for the Dusky-capped Flycatchers of all of the Yucatán Peninsula and Isla Cozumel. The type locality of *platyrhynchus* is Isla Cozumel, so the mainland subspecies remains to be named. It may be called:

Myiarchus tuberculifer manens, new subspecies

Holotype.—CM 144800, male just completing first prebasic molt, from ca. 20 km E of Chicxulub Puerto, Yucatán, México, collected by Juan Nava S. for Kenneth C. Parkes, on 2 December 1971 (field no. KCP 3232).

Characters.—Similar to *M. t. platyrhynchus* of Isla Cozumel, but dorsum paler, more greenish-olive (less sooty brown), contrasting more with the dark crown; reddish brown of upper tail coverts, outer webs of unworn rectrices, wing coverts, and secondaries paler. Yellow of posterior underparts much richer and more extensive—in *platyrhynchus* the gray of the upper breast extends farther caudad centrally and also blends gradually with the yellow of the lower breast; in addition, the sides and flanks of *platyrhynchus* are washed with grayish olive, narrowing the pure yellow area. In older and seasonally faded specimens of *manens*, the yellow may fade to the pale color typical of *platyrhynchus*, but such specimens are immediately recognizable by the greater extent of yellow on the underparts. The axillars and under wing coverts of *manens* are yellow, those of *platyrhynchus* white or nearly so. In *manens* there is a tendency for the throat to appear light gray streaked vaguely with white; the throat of *platyrhynchus* is paler gray and more uniform. The lower mandible of *manens* is brownish in

←

Fig. 1.—Principal localities mentioned in text. B = Belize; C = Campeche, México; CH = Chiapas, México; H = Honduras; P = Petén, Guatemala; Q = Quintana Roo, México; T = Tabasco, México; V = Veracruz, México; Y = Yucatán, México; I = Bay Islands; 2 = Belize City; 3 = Camp Mengel; 4 = Cauquira; 5 = Champotón; 6 = Chetumal; 7 = Chichén Itzá; 8 = Chicxulub Puerto; 9 = Ciudad Campeche; 10 = Coyame; 11 = Escárcega; 12 = Felipe Carrillo Puerto; 13 = Ichek; 14 = Isla Cancún; 15 = Isla Cozumel; 16 = Isla del Carmen; 17 = Laguna Chacabacab; 18 = Laguna Ocotil; 19 = La Vega; 20 = Matamoros; 21 = Mérida; 22 = Pacaitún; 23 = Progreso; 24 = Puerto Morelos; 25 = Sabancuy; 26 = Sontecomapan; 27 = Tabi; 28 = Temax; 29 = Tikal; 30 = Tlacotalpan; 31 = Xcopan; 32 = Xpujil.

life, thus differing from that of *platyrhynchus* and of *connectens* and *lawrenceii*, the adjacent mainland races, which are black.

Range.—All but the base of the Yucatán Peninsula, México. See *Remarks*, below, for a discussion of intergradation.

Etymology.—From the Latin verb *maneo*, to remain or stay in place, in reference to its non-migratory status as contrasted with *M. t. platyrhynchus*.

Remarks.—As mentioned in the introductory remarks on this species, true *platyrhynchus* of Isla Cozumel leaves its breeding ground for the winter, as is also true of *M. tyrannulus cozumelae*. The wintering area of neither subspecies is known, but there is one indication of the migration route of *platyrhynchus*. Monroe (1968:283) reported a specimen of *Myiarchus tuberculifer* he collected on 13 April 1964 in a mangrove swamp near Cauquira, on Laguna Caratasca, just inland from the northeasternmost coast of Honduras. This specimen, a male "in breeding condition," he was unable to separate from "examples of *M. t. platyrhynchus* Ridgway from the Yucatán Peninsula and [it] extends the known range of this race south of British Honduras." As indicated by Monroe's map, such a "range extension" would result in a totally disjunct pattern, as the remainder of Caribbean Honduras is occupied by the subspecies *connectens* Miller and Griscom. Monroe, of course, was aware neither that "*platyrhynchus*" as then understood was a composite nor that true *platyrhynchus* of Isla Cozumel is migratory. I have examined his specimen (LSU 32348) and find that it matches Cozumel specimens in every respect. The fact that his specimen was in "breeding condition" can be explained by the late date; Nelson and Goldman (specimens in USNM) found Dusky-capped Flycatchers already on Isla Cozumel 4–8 April 1901. Monroe's bird would have had about 670 km farther to fly if it had gone on a direct diagonal from the collecting locality across the Caribbean to Isla Cozumel, or about 1150 km if it followed the coastline west to the end of the Gulf of Honduras and then turned north along the Belize and Quintana Roo coasts. We still lack information as to the true winter range of *platyrhynchus*.

The range of *manens* adjoins that of *connectens* at the base of the Yucatán Peninsula. The latter race differs from both *manens* and *platyrhynchus* in having the outer edge of the inner webs of the rectrices distinctly rufous, as well as in having a darker back and a decidedly darker and more contrasting crown. It also has the throat darker, less whitish gray than in *manens*. The first signs of intergradation appear in the interior of Quintana Roo. Three poorly-made skins (March, May, June; 2 Tabi, 1 Felipe Carrillo Puerto) from this area are faintly darker on the crown than similarly worn specimens from Chichén Itzá, in the interior of the state of Yucatán to the north, but otherwise they

show no approach to *connectens*. Of eight skins from southeastern Quintana Roo (vicinity of Chetumal; Xcopan; Camp Mengel; Laguna Chacanbacab), four show very narrow reddish-brown edgings on the inner webs of the rectrices. All are darker and somewhat browner dorsally than more northern birds, all have darker throats, and most have the crowns darker and contrasting more with the back. These character states are not necessarily coordinated. The specimen with the least *connectens*-like crown is YPM 8722, from 46 km W of Chetumal, 15 February 1949. It is also relatively pale and less brownish dorsally than most of this series, but is one of the four with narrow rufous inner margins to the rectrices. YPM 8721, from Laguna Chacanbacab, 14 May 1949, in spite of the late spring date when fading would be expected, is the darkest and brownest dorsally of the series, but it lacks the rectrix edgings. The whole series can be considered to be intergrades between *manens* and *connectens*, which is compatible with Russell's (1964) identification of most of the Dusky-capped Flycatchers from Belize south to about Belize City as intergrades (although one specimen from Corozal, near Chetumal, he called "*platyrhynchus*" [= *manens*]).

The northernmost specimen examined from the state of Campeche is one from Ichek (YPM 13796), which is typical of *manens*. Two from San José Carpizo, 45 km S of Ciudad Campeche (UMMZ 155762–3) also belong here. Farther south, one of three specimens from 8–32 km W of Escárcega and one from La Tuxpeña have traces of rufous on the inner webs of the rectrices and are slightly darker on the crown than typical *manens*, but are closest to that race. Their intergradation is with *connectens* rather than with the similarly colored but much larger race *lawrencei* (Giraud) of the Caribbean slope of México to the west, as the intergrades are identical in size with both *manens* and *connectens*. Following the coast south and west from Ciudad Campeche, a specimen from Champotón is nearest *manens* dorsally, but has narrow distinct rufous inner edges to the rectrices and a slightly darker throat. One from Sabancuy, however, does not differ from *manens*. An excellent series of 13 January and February specimens from Isla del Carmen is quite variable in all color characters but not in size, and must therefore be considered *manens* \geq *connectens*. Finally, a specimen from La Curva, 34 km E of the Tabasco border, is similarly intermediate.

Three specimens from Tikal, Petén, Guatemala, about 60 km S of the Campeche border (MCZ) are *connectens*. Smithe and Paynter (1963) called these "*platyrhynchus*" [= *manens*], stating that all lacked "rufous markings on the underside of the rectrices." All are very dark and brownish dorsally and have blackish caps. One September specimen (MCZ 262919) has (contra Smithe and Paynter, 1963) obvious

rufous edges to the inner webs of the rectrices, whereas in a June specimen (260992) these have been almost completely worn away. Another June skin (260993), with a surprisingly unworn tail, lacks the rufous on the tail, and in this respect resembles some of the Belize skins that are otherwise typical of *connectens*. A single skin from the ruins of Chicama, 8 km W of Xpujil, southeastern Campeche, 8 August 1978 (UW A20278), in heavy molt, is indistinguishable from *connectens*.

Paynter (1957) showed that the Dusky-capped Flycatchers of Laguna Ocotál, in easternmost Chiapas near southwestern Petén, are *connectens*; Traylor (1979) mentioned Chiapas only in the range of *lawrenceii*.

Paynter (1957) referred several times to *connectens* as larger than "*platyrhynchus*" [= *manens*], and measurements published by Brodorb (1943) show only 1 mm overlap in wing measurements of these two races. The specimens assembled for this study, however, show only a slight difference in mean in both wing length and weight between the two races, with the extremes almost identical. The overemphasis on size as a character separating *manens* and *connectens* is exemplified by Smithe and Paynter (1963), who, as mentioned above, identified their five Tikal specimens as "*platyrhynchus*." I have seen three of these, and all three matched *connectens* perfectly in all color characters with the exception of one specimen that lacked rufous on the inner margins of the rectrices. Smithe and Paynter stated that their series "is quite dark, thereby approaching *M. t. connectens*, but all the specimens are small . . ." (emphasis added). Rather than the small size being an indication of the necessity of identifying these dark birds as "*platyrhynchus*," it is simply further evidence that the size difference between the Yucatán subspecies and *connectens* is insignificant. Paynter's specimens from Laguna Ocotál, Chiapas, which averaged slightly larger than Yucatán Peninsula specimens in both weight and wing length, may have been affected by introgression from *lawrenceii*. The two subspecies *lawrenceii* and *connectens* differ only in size, with northern examples of the former being decidedly larger than *connectens*. Traylor (1979) mentioned only El Salvador as an area of intergradation between the two, and gave the range of *lawrenceii* as extending to "Tobasco and Chiapas, and highlands of Guatemala." The intergradation in size between *lawrenceii* and *connectens* is more clinal than this range description would suggest, and begins farther north than indicated by Traylor, as already shown by Wetmore (1943) and Brodorb (1943), extending to southern Veracruz. This is confirmed by specimens examined in this study; those from Tlacotalpan and Son-tecomapan, southern Veracruz, were smaller than *lawrenceii* from northeastern México but larger than Honduras specimens of *connectens*.

Paynter (1957) was correct in stating that "*platyrhynchus*" tends to have a paler "bill" [=lower mandible] than *connectens* or *lawrenceii*, but only if this statement is restricted to the *manens* or mainland component of Paynter's composite "*platyrhynchus*." In true *platyrhynchus* of Isla Cozumel, the USNM series taken by Nelson and Goldman in 1901 has pale brown lower mandibles, but in specimens taken between 1962 and 1979, the lower mandibles are black. In *manens* of the peninsular mainland, however, pale lower mandibles are not correlated with museum age, as indicated by color notes taken at the time of collecting by Paynter and by A. R. Phillips; in these, the lower mandibles are quite consistently brownish. I agree with Russell (1964) that this character is not wholly diagnostic. There is so much variation in the color of *dried* (specimen) bills that the character is of little use in evaluating intergradation when original color notes are lacking (as is usually the case). The separation of *M. t. platyrhynchus*, *manens*, and *connectens* by plumage color is sufficiently clearcut for bill color to be unnecessary for definition of these races.

Specimens examined.—*M. t. lawrenceii* (+ *lawrenceii* × *connectens*): MÉXICO: Tamaulipas: Río Corona, 1; Victoria, 1. Nuevo León: Mesa de Chipinque, 1. Hidalgo: Jacala, 1. Veracruz: Coyamé, 5; Sontecomapan (1 mi NW), 2; Tlacotalpan (7–8 mi E), 2. *M. t. connectens*: MÉXICO: Campeche: Ruins of Chicama, 1. GUATEMALA: Petén: Tikal, 3. BELIZE: various localities, all S of Belize City, 19. HONDURAS: various localities, 38. *M. t. connectens* × *manens*: MÉXICO: Campeche: Champotón, 1; Isla del Carmen, 14; La Curva, 1. Quintana Roo: Camp Mengel, 1; Chetumal and vicinity, 5; Laguna Chacanbacab, 1; Xcopan, 1. *M. t. manens*: MÉXICO: Campeche: Escárcega (8–32 km W), 3; Ichek, 1; La Tuxpeña, 1; Sabancuy, 1; San José Carpizo, 2. Yucatán: Chichén Itzá, 23; Chicxulub Puerto and vicinity, 4; Progreso (1–16 mi E), 5; Sisal, 3; Uxmal, 2. Quintana Roo: Felipe Carrillo Puerto, 1; Kantunil-kin (15 km NW), 1; La Vega, 1; Xcan, 2. *M. t. platyrhynchus*: MÉXICO: Quintana Roo: Isla Cozumel (various localities), 14. HONDURAS: Gracias a Dios: Cauquira (1 mi SE), 1.

DISCUSSION

Of the three *Myiarchus* flycatchers sympatric on the island of Jamaica, one (*M. validus*) is a well differentiated species that has even been generically separated in the past; one (*M. barbirostris*) is closely related to the widespread *M. tuberculifer* but considered a separate species because of differences in vocalizations; and one (*M. stolidus*) is a member of a West Indian superspecies of unknown mainland affinities (Lanyon, 1967). In contrast, all three of the sympatric *Myiarchus* on Isla Cozumel are only subspecifically differentiated from their representatives on the adjacent mainland of the Yucatán Peninsula. Two (*M. tyrannulus cozumelae* and *M. tuberculifer platyrhynchus*) are migratory on Isla Cozumel, although the mainland representative of the latter (*M. tuberculifer manens*) is not. The third Cozumel form, *M. yucatanensis lanyoni*, is an exceptionally distinctly differentiated insular representative of a relict species of uncertain affinities within

the genus; like its mainland relatives, *M. y. lanyoni* is non-migratory. The Isla Cozumel subspecies of *Myiarchus yucatanensis* was described as differing from the nominate population of the mainland in being very much darker (blackier) dorsally; in having the rufous markings of wings and tail darker; in having the gray of the lower breast less pure and more extensive posteriorly, extending along the sides and flanks such that the yellow area of the abdomen is restricted; and in having the under wing coverts and axillars "dull yellowish white rather than light yellow." As stated earlier in the present paper, examination of additional specimens has shown that the yellow of the underparts is distinctly paler than in specimens of the nominate race of comparable season and museum age. Although differing in degree of differentiation, each of these character states is matched in the Isla Cozumel populations of *M. tyrannulus* and *M. tuberculifer*. In both, the Cozumel subspecies is darker and browner, less greenish dorsally; the rufous areas of upper tail coverts, wings and tail are darker (except for the wings of *M. tyrannulus cozumelae*, in which the rufous is not darker, and the tail of *M. tuberculifer platyrhynchus*, which, like mainland *manens*, lacks significant rufous areas); the gray of the lower breast is more extensive and blends more with the adjacent yellow; the yellow is paler; and the axillars (and under wing coverts in *M. tuberculifer platyrhynchus*) are white or whiter, less yellowish.

Parallel geographic variation in color in congeneric species has been described for several birds. Of the Downy Woodpecker (*Picoides pubescens*) of North America, Baird et al. (1874) wrote: "The remarks already made on the variation of [the Hairy Woodpecker, *P. villosus*] apply equally well here; all the differences in size and markings with locality being almost exactly reproduced." Snow (1954) called attention to parallel patterns of color variation in *Parus cristatus*, *P. palustris*, and *P. montanus* in Europe. Such variation is often associated with fairly obvious environmental conditions—for example, the desert-colored larks of North Africa (cf. *Galerida cristata* and *G. theklae*; Etchécopar and Hüe, 1964) and the heavily pigmented races of the above-mentioned Downy and Hairy woodpeckers in the humid Pacific Northwest of North America. However, there is no obvious major difference between the environmental conditions on Isla Cozumel and the adjacent Yucatán Peninsula mainland that could be correlated with the color trends visible in *Myiarchus*. Paynter (1955) recognized Isla Cozumel endemic subspecies of the following Yucatán Peninsula species (excluding those of West Indian affinities or of questionable Cozumel provenience): *Buteo magnirostris*, *Crax rubra*, *Chlorostilbon canivetii*, *Melanerpes aurifrons*, *M. pygmaeus*, *Attila spadiceus*, *Melanoptila*

glabrirostris, *Polioptila caerulea*, *Cyclarhis gujanensis*, *Piranga roeogularis*, *Cardinalis cardinalis*, and *Tiaris olivacea*. Of these, the *Crax* and *Melanoptila* differ from the mainland populations only in size, and the *Chlorostilbon* in tail proportions. In *Piranga* and *Cardinalis* there is geographic variation on the mainland; the Cozumel population of *Piranga* is nearer the darker mainland race, whereas that of *Cardinalis* is nearer the paler mainland race. The *Tiaris* differs from the mainland race in having less extensive black on the underparts of males. Only in *Buteo*, both *Melanerpes*, *Attila*, *Polioptila*, and *Cyclarhis* can the Cozumel populations be broadly characterized as darker dorsally than those of the mainland, and these differ sufficiently *inter se* as to the manifestation of richer pigmentation that it is doubtful that they represent any trend that is common to the three *Myiarchus* species. One looks in vain for any counterpart to the pale yellow underparts of the three Cozumel *Myiarchus* races.

It is clear that within the rather uniform genus *Myiarchus*, selection has operated on three species (not especially closely related *within* the genus) on Isla Cozumel in virtually identical fashion. Other Cozumel endemic subspecies show little or no evidence of similar responses to selection. The environmental factors to which the parallel trends in differentiation in *Myiarchus* have responded remain obscure.

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ARTICLE 2

SYSTEMATIC REVIEW OF THE ANTILLEAN BATS OF THE *NATALUS MICROPUS*-COMPLEX (CHIROPTERA: NATALIDAE)

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ABSTRACT

Nongeographic and geographic morphometric variation in Antillean populations of bats of the *Natalus micropus*-complex were analyzed using univariate and multivariate statistical techniques. Samples of males and females from Jamaica and the Dominican Republic revealed females to be significantly larger than males in three measurements and males were significantly larger than females in two measurements. Generally, low coefficients of variation were found in samples of both sexes. The highest value obtained was 5.7 for length of phalanx 1 (digit III) in the sample from Old Providence Island. Two species—*Natalus micropus* and *N. tumidifrons*—were recognized within this complex. The chief difference between the species was the larger overall size of *N. tumidifrons*. *N. tumidifrons* is confined to the Bahamas and is considered to be monotypic. Two subspecies are recognized in *N. micropus* with the nominate subspecies occurring on Old Providence Island, Jamaica, and Hispaniola, and *N. m. macer* on Cuba and the Isle of Pines.

INTRODUCTION

The bats of the genus *Natalus* belong to the monotypic family Natalidae. In the West Indies members of the genus occur on the Greater and Lesser Antilles, the Bahamas, and Old Providence Island (off the

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Caribbean coast of Nicaragua). On the continental mainland they occur from Mexico to Brazil as well as on the coastal islands of Trinidad and Curaçao, off the northern coast of South America. Beginning with the description of *Natalus stramineus* by Gray in 1838, the taxonomic history of the family Natalidae has been characterized by a degree of confusion for most of the first century of chiropteran classification. During this period, the genus *Natalus*, usually allied with *Furipterus* and *Thyroptera*, was variously placed in the Phyllostomidae, Vespertilionidae, Emballonuridae, and Noctilionidae. In 1899 Miller, supported by conclusions of H. Allen (1892, 1894), proposed the Natalidae as a family containing *Chilonatalus* and *Amorphochilus* in addition to the above genera. In the same paper, Miller (1899) also reviewed the taxonomic history of the family up to that date. Miller (1906) described and added the new genus *Phodotes* to the family and a year later (Miller, 1907) grouped it with *Natalus*, *Chilonatalus*, and *Nyctiellus* in the Natalidae, placing *Furipterus* and *Amorphochilus* in the Furipteridae, and *Thyroptera* in the Thyropteridae.

Based on anatomical characteristics, Winge (1941) relocated the Natalidae as a division (Natalini) of the Vespertilionidae, including the genera "*Natalis*," *Thyroptera*, *Myzopoda*, *Amorphochilus*, and *Furia* (*Furipterus*), and suggesting also that they originated in the Old World. The taxonomic arrangement by Miller (1907) was reevaluated by Simpson (1945), who modified it by reducing *Chilonatalus* and *Phodotes* to subgenera of *Natalus*, thus leaving the Natalidae with two genera (*Natalus* and *Nyctiellus*). In perhaps the most significant contribution after Miller (1899, 1907), Dalquest (1950) discussed the taxonomic status of the genera of Natalidae and concluded that there was only a single genus in the family, *Natalus*, with three subgenera, *Natalus* (including *Phodotes*), *Chilonatalus*, and *Nyctiellus*. In his review, Dalquest also predicted the reduction of some nominal species within the genus to subspecific level. This arrangement was followed by Cabrera (1957), who, in addition to *Phodotes*, suggested that *Chilonatalus* was inseparable from *Natalus* even as a subgenus.

Although Hall and Kelson (1959) suggested that the nominal forms of the subgenus *Chilonatalus* (Miller, 1898)—*Natalus micropus* (Dobson, 1880) from Jamaica, *N. brevimanus* (Miller, 1898) from Old Providence Island, *N. tumidifrons* (Miller, 1903) from the Bahamas, and *N. macer* (Miller, 1914) from Cuba and Isle of Pines—might be only subspecific forms of *micropus*, they were treated as distinct species by these authors. Later, Varona (1974) without presenting any additional evidence treated all of these forms as subspecies of *N. micropus* and adopted the suggestion of Cabrera (1957) to not recognize the subgenus *Chilonatalus*. Finally, this arrangement has been followed by Hall (1981) without additional consideration.

In the last revision of natalid bats (Goodwin, 1959), only the larger forms belonging to the subgenus *Natalus* were included. Recently Kerridge and Baker (1978) have pointed out the need for a revision of the taxonomic status of the bats of *Natalus micropus*-complex. The aims of this study were to analyze in detail variation throughout the geographical range of the group. Univariate and multivariate analyses were used to examine the relationship among the populations involved.

METHODS AND MATERIALS

A total of 229 specimens was examined during this study. Most of them were conventional museum specimens preserved as skins and skulls, and specimens in alcohol with skulls removed. Additional material examined included complete skeletons, skin only, skull only, and complete fluid-preserved specimens.

External and cranial measurements were taken by means of dial calipers. All measurements are given in millimeters. Measurements were taken as follows: *length of forearm*—from the posteriormost projection of the elbow to the anteriormost portion of the wrist joint with the wing flexed; *length of metacarpal III*—distance from the wrist to the distal end of the third metacarpal; *length of the phalanx 1 (digit III)*—distance from the proximal to the distal end of the first phalanx of digit III; *greatest length of skull*—greatest distance from the anteriormost projection of the incisors to the posterior portion of the occipital bone; *condylobasal length*—distance from the posteriormost projection of exoccipital condyles to the anteriormost projection of premaxillae; *zygomatic breadth*—greatest width across zygomatic arches at right angles to longitudinal axis of cranium; *postorbital breadth*—least width across postorbital constriction, measured at right angles to the long axis of the cranium; *breadth of braincase*—greatest width across braincase, measured at right angles to the long axis of the cranium; *mastoid breadth*—greatest width across mastoid processes, measured at right angles to the long axis of the cranium; *length of maxillary toothrow*—distance from the posterior lip of alveolus of M³ to the anterior lip of alveolus of canine; *breadth across upper molars*—greatest distance from labial margins of the upper molars at the widest point; *depth of braincase*—distance from the line along the flat part of the braincase to a line on the midventral part of the cranium touching the palate and the basioccipital.

Based on their geographical distribution, all adult specimens examined were grouped in five samples for males and females as follows: Bahamas; Cuba, including Isle of Pines; Jamaica; Dominican Republic; Old Providence Island. Statistical analyses were performed on an IBM-360 computer at Carnegie-Mellon University and a DEC-10 computer at the University of Pittsburgh. Univariate analyses were performed using the UNIVAR program. This program yields standard statistics (mean, range, standard deviations, standard error of the mean, variance, and coefficient of variation), and employs a single classification analyses of variance (ANOVA; F-test, significance level 0.05) to test for significant differences between or among means (Sokal and Rohlf, 1969). In addition, multivariate analyses were performed for both sexes to determine the degree of divergence among samples. Stepwise discriminant analysis and canonical analysis (BMDP7M, Dixon and Brown, 1977) perform a multiple discriminant analysis in a stepwise manner, selecting the variable entered by finding the variable with the greatest F value. The F value for inclusion was set at 0.01, and the F value for deletion was set at 0.05. Canonical coefficients were derived by multiplying the coefficient of each discriminant function by the mean of each corresponding variable. The program also classifies individuals, placing them with the group that they are nearest to on the discriminant functions.

RESULTS

Nongeographic Variation

Two kinds of nongeographic variation are discussed—secondary sexual variation and individual variation. Because of the limited size of the samples available, variation with age could not be analyzed.

Secondary sexual variation.—Using single classification analysis of variance, males were tested against females of two geographical samples (Jamaica and Dominican Republic) to learn if the sexes were significantly different in the characters studied. The results of these analyses (Table 1) demonstrated that in the 12 external and cranial measurements tested, females were significantly larger than males in two measurements (length of forearm and length of metacarpal III) in specimens from both samples and in one measurement (length of phalanx 1, digit III) in specimens from the Dominican Republic. The means for females averaged 0.1 mm larger in condylobasal length in specimens from both islands, and in length of phalanx 1 (digit III) and greatest length of skull in specimens from Jamaica and Dominican Republic, respectively. Of the remaining seven measurements, the sexes averaged the same in four (zygomatic breadth, postorbital breadth, length of maxillary toothrow, and breadth across upper molar). Males from both samples were significantly larger than females in depth of braincase, and in breadth of braincase in specimens from Jamaica. Males from the Dominican Republic were also 0.1 mm larger than females in mastoid breadth.

In conclusion, specimens from both samples reveal secondary sexual variation in size, and therefore, males and females were treated separately for analysis of geographic variation.

Individual variation.—In general, low coefficients of variation were found for all the characters studied in both sexes in samples from Jamaica and Dominican Republic (Table 1), as would be expected for minute-sized bats (Long, 1968, 1969) such as *Natalus*. Although external measurements generally have relatively high individual variation, depth of braincase (CV, 1.9 to 4.2) was found to vary most among the 12 external and cranial characters studied. The remaining measurements had coefficient values of 3.8 or less.

In the analysis of geographical variation of all samples (Table 2), additional coefficients of variation were obtained. For all samples, variation in external measurements was found to be higher (1.6 to 5.7) than in cranial measurements (0.9 to 4.2). The highest individual variation was found in length of metacarpal III (5.6) and length of phalanx 1 (digit III) (5.7), both from the Old Providence Island sample. Of cranial measurements, depth of braincase (1.2 to 4.2), postorbital constriction (1.8 to 4.2), and breadth across upper molar (1.9 to 4.2)

showed the highest individual variation, whereas condylobasal length (1.1 to 2.2) and mastoid breadth (1.1 to 1.9) showed the least.

Geographic Variation

In order to establish the relationship of the populations involved in this study, univariate and multivariate analyses were utilized to compare the geographical samples (with the exception of males from Cuba and females from Bahamas, that could not be satisfactorily tested due to insufficient sample size).

Univariate Analyses.—Standard statistics for samples of males and females from each geographical sample and the results of the SS-STP analyses for determination of the maximally non-significant subsets of each variable are given in Table 2. These results indicate that males from the Bahamas grouped in one subset differing significantly from all other samples in the following characters: length of phalanx 1 (digit III); greatest length of skull; condylobasal length; zygomatic breadth; postorbital constriction; mastoid breadth; breadth of braincase; length of maxillary toothrow; mastoid breadth; breadth across upper molars. In the remaining two measurements, the Bahamas sample also averaged larger although not significantly. The sample of females from the Bahamas did not contain enough individuals to be entered in the analyses, but the two available females averaged larger than other samples in all measurements studied. In six cranial measurements (greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, length of maxillary toothrow, and breadth across upper molars) for males and seven for females (the same six as for males plus breadth of braincase), there was no overlap in the range of measurements for the sample from the Bahamas and the samples from the other islands.

The remainder of the samples grouped into varying numbers of overlapping subsets. Particularly, the samples from Cuba and Jamaica were intermediate in some characters between the Bahamas and other samples. Females from Cuba averaged larger than other samples in three measurements; and the males available, although not enough to be entered in the analyses, averaged larger than specimens from other samples in six measurements. The Jamaica sample averaged larger in three characters for males and four characters for females than the remaining samples. Both samples were however, grouped in most variables with the samples from the Dominican Republic and Old Providence Island.

Length of phalanx 1 (digit III) (females), greatest length of skull (females), and depth of braincase (males) showed the broadest overlap of subsets. Forearm (females), greatest length of skull (males), and

Table 1.—*Secondary sexual variation in external and cranial measurements of samples of the Natalus micropus-complex from Jamaica and the Dominican Republic. Statistics given are number, mean, two standard errors, range, coefficient of variation and F_s value. Means for males and females that are significantly different at $P < 0.05$ level are marked with an asterisk.*

Locality	Sex	N	Mean	(Range) + 2 SE	CV	(F _s)
<i>Length of forearm</i>						
Jamaica	♂	21	34.0	(32.5–35.2) + 0.31	2.1	8.269*
Jamaica	♀	41	34.6	(32.6–36.1) + 0.21	1.9	
Dominican Republic	♂	32	32.9	(30.6–34.4) + 0.28	2.4	7.296*
Dominican Republic	♀	11	33.6	(32.6–35.3) + 0.50	2.5	
<i>Length of metacarpal III</i>						
Jamaica	♂	21	31.8	(30.2–33.1) + 0.32	2.3	15.541*
Jamaica	♀	41	32.6	(30.8–34.1) + 0.25	2.4	
Dominican Republic	♂	32	30.7	(29.2–31.9) + 0.25	2.3	4.113*
Dominican Republic	♀	10	31.2	(30.5–32.4) + 0.44	2.2	
<i>Length of phalanx 1 (digit III)</i>						
Jamaica	♂	21	13.6	(12.7–14.3) + 0.20	3.4	1.770
Jamaica	♀	41	13.7	(12.6–15.2) + 0.16	3.7	
Dominican Republic	♂	32	12.9	(12.1–13.6) + 0.15	3.3	9.056*
Dominican Republic	♀	10	13.4	(12.6–14.2) + 0.30	3.6	
<i>Greatest length of skull</i>						
Jamaica	♂	16	14.3	(13.9–15.0) + 0.13	1.8	0.226
Jamaica	♀	38	14.3	(14.0–14.8) + 0.06	1.3	
Dominican Republic	♂	31	14.1	(13.6–14.5) + 0.07	1.5	2.697
Dominican Republic	♀	11	14.3	(13.9–14.6) + 0.11	1.3	
<i>Condylbasal length</i>						
Jamaica	♂	13	12.4	(12.1–12.9) + 0.11	1.5	0.782
Jamaica	♀	33	12.5	(12.1–12.8) + 0.67	1.5	
Dominican Republic	♂	31	12.4	(12.2–12.7) + 0.05	1.2	0.814
Dominican Republic	♀	11	12.5	(12.3–12.7) + 0.09	1.2	
<i>Zygomatic breadth</i>						
Jamaica	♂	13	6.5	(6.3–6.6) + 0.04	1.2	0.245
Jamaica	♀	35	6.5	(6.0–6.7) + 0.05	2.2	
Dominican Republic	♂	30	6.5	(6.1–6.7) + 0.05	2.1	0.064
Dominican Republic	♀	10	6.5	(6.1–6.6) + 0.10	2.4	
<i>Postorbital breadth</i>						
Jamaica	♂	16	2.6	(2.5–2.9) + 0.05	3.8	0.006
Jamaica	♀	39	2.6	(2.5–2.8) + 0.02	2.7	
Dominican Republic	♂	32	2.7	(2.5–2.9) + 0.03	3.3	0.507
Dominican Republic	♀	11	2.7	(2.6–2.9) + 0.06	3.8	
<i>Breadth of braincase</i>						
Jamaica	♂	16	6.0	(5.8–6.2) + 0.06	2.1	7.149*
Jamaica	♀	38	5.9	(5.7–6.1) + 0.03	1.6	
Dominican Republic	♂	32	6.0	(5.7–6.3) + 0.05	2.4	2.347
Dominican Republic	♀	11	6.0	(5.8–6.2) + 0.07	2.0	

Table 1.—*Continued.*

Locality	Sex	N	Mean	(Range) + 2 SE	CV	(F _s)
<i>Mastoid breadth</i>						
Jamaica	♂	12	6.3	(6.2–6.4) + 0.05	1.4	0.085
Jamaica	♀	33	6.3	(6.1–6.5) + 0.04	1.6	
Dominican Republic	♂	32	6.4	(6.2–6.6) + 0.04	1.9	1.073
Dominican Republic	♀	10	6.3	(6.2–6.5) + 0.06	1.5	
<i>Length of maxillary toothrow</i>						
Jamaica	♂	15	5.9	(5.7–6.1) + 0.05	1.6	0.027
Jamaica	♀	38	5.9	(5.7–6.1) + 0.04	1.9	
Dominican Republic	♂	31	5.9	(5.6–6.1) + 0.04	1.9	2.092
Dominican Republic	♀	11	5.9	(5.8–6.0) + 0.04	1.1	
<i>Breadth across upper molars</i>						
Jamaica	♂	16	4.3	(4.1–4.4) + 0.05	2.2	0.163
Jamaica	♀	38	4.3	(4.0–4.6) + 0.04	3.0	
Dominican Republic	♂	31	4.4	(4.2–4.6) + 0.03	2.0	0.625
Dominican Republic	♀	11	4.4	(4.2–4.5) + 0.05	2.0	
<i>Depth of braincase</i>						
Jamaica	♂	16	5.0	(4.8–5.2) + 0.06	2.5	8.744*
Jamaica	♀	38	5.0	(4.7–5.2) + 0.03	3.0	
Dominican Republic	♂	32	5.0	(4.7–6.2) + 0.07	4.2	6.025*
Dominican Republic	♀	11	4.8	(4.7–5.0) + 0.06	1.9	

length of maxillary toothrow (females) were the characters with least overlap. The remainder of the characters, 10 for males and two for females, showed the samples studied grouping in non-overlapping subset.

Because the population *Natalus* from the Dominican Republic was not previously known, we compared samples from the Jamaica and Dominican Republic populations with the following results (Table 1). Males from Jamaica were significantly larger than males from the Dominican Republic in the three external measurements and 0.2 mm larger in greatest length of skull, whereas males from the Dominican Republic were 0.1 mm larger than the Jamaica sample in postorbital breadth, mastoid breadth, and breadth across upper molars. In the remaining five measurements, both samples averaged the same. In the case of females, Jamaican populations were significantly larger from those of the Dominican Republic in four measurements (length of forearm, length of metacarpal III, length of phalanx 1 (digit III), and depth of braincase. In three of the remaining measurements (postorbital constriction, breadth of braincase, and breadth across upper molars), females from the Dominican Republic averaged 0.1 mm larger than those

Table 2.—*Geographic variation in external and cranial measurements of 10 samples (five samples of males, and five samples of females) of the Natalus micropus-complex. Statistics given are sample size, mean, two standard errors of the mean, range, coefficient of variation, F-value, critical F-value, and results of SS-STP analysis showing nonsignificant subsets. Groups of means not significantly different at the 5% level are marked ns.*

Sex and locality	N	Mean \pm 2 SE	Range	CV	F, F'	Results SS-STP
<i>Length of forearm</i>						
Male						
Bahamas	6	34.1 \pm 0.49	33.2–34.7	1.8	12.18	I
Jamaica	16	34.0 \pm 0.38	32.5–35.2	2.3	2.76	I
Dominican Republic	32	32.9 \pm 0.28	30.6–34.4	2.4		I
Old Providence	8	32.5 \pm 0.60	30.7–33.4	2.6		I
Cuba	8	32.7	32.2–33.1			
Female						
Jamaica	37	34.6 \pm 0.22	32.6–36.1	2.0	19.58	I
Dominican Republic	11	33.6 \pm 0.50	32.6–35.3	2.5	2.76	I
Old Providence	4	33.1 \pm 0.53	32.3–33.5	1.6		I I
Cuba	5	32.4 \pm 0.70	31.0–32.9	2.4		I
Bahamas	2	33.5	33.5			
<i>Length of metacarpal III</i>						
Male						
Bahamas	6	32.2 \pm 0.59	31.0–33.1	2.3	9.884	I
Jamaica	16	31.8 \pm 0.39	30.2–33.1	2.4	2.76	I
Dominican Republic	32	30.7 \pm 0.25	29.2–31.9	2.3		I
Old Providence	8	30.3 \pm 1.20	26.2–31.4	5.6		I
Cuba	8	31.3	30.3–32.4			
Female						
Jamaica	37	32.7 \pm 0.26	30.8–34.1	2.5	16.001	I
Old Providence	4	31.5 \pm 0.59	30.6–31.9	1.9	2.76	I
Dominican Republic	10	31.2 \pm 0.44	30.5–32.4	2.2		I
Cuba	5	30.8 \pm 0.72	30.0–32.1	2.6		I
Bahamas	2	33.0	32.8–33.2			
<i>Length of phalanx I (digit III)</i>						
Male						
Bahamas	6	14.7 \pm 0.34	14.3–15.3	2.8	30.161	I
Jamaica	16	13.6 \pm 0.23	12.9–14.3	3.4	2.76	I
Dominican Republic	32	12.9 \pm 0.15	12.1–13.6	3.3		I
Old Providence	8	12.8 \pm 0.51	11.2–13.8	5.7		I
Cuba	8	13.9	13.6–14.6			
Female						
Cuba	4	14.3 \pm 0.52	13.7–14.9	3.6	3.740	I
Jamaica	37	13.7 \pm 0.17	12.6–15.2	3.9	2.76	I I
Old Providence	4	13.4 \pm 0.39	13.0–13.8	2.9		I I
Dominican Republic	10	13.4 \pm 0.30	12.6–14.2	3.6		I
Bahamas	2	14.7	14.4–14.9			

Table 2.—Continued.

Sex and locality	N	Mean \pm 2 SE	Range	CV	F _s F	Results SS-STP
<i>Greatest length of skull</i>						
Male						
Bahamas	6	15.6 \pm 0.20	15.2–15.9	1.6	71.264	I
Jamaica	16	14.3 \pm 0.13	13.9–15.0	1.8	2.76	I
Dominican Republic	31	14.1 \pm 0.07	13.6–14.5	1.5		I I
Old Providence	8	13.9 \pm 0.18	13.5–14.3	1.9		I
Cuba	2	14.6	14.4–14.8			
Female						
Jamaica	37	14.3 \pm 0.06	14.0–14.8	1.3	4.903	I
Dominican Republic	11	14.3 \pm 0.11	13.9–14.6	1.3	2.76	I I
Cuba	5	14.2 \pm 0.38	13.5–14.6	3.0		I I
Old Providence	3	13.8 \pm 0.55	13.3–14.2	3.4		I
Bahamas	2	15.6	15.4–15.8			
<i>Condylbasal length</i>						
Male						
Bahamas	6	13.8 \pm 0.12	13.6–14.0	1.1	136.135	I
Jamaica	13	12.4 \pm 0.11	12.1–12.9	1.5	2.76	I
Dominican Republic	31	12.4 \pm 0.05	12.2–12.7	1.2		I
Old Providence	5	12.2 \pm 0.15	12.1–12.5	1.4		I
Cuba	1	12.6				
Female						
Cuba	4	12.7 \pm 0.17	12.5–12.9	1.3	2.339	ns
Old Providence	3	12.5 \pm 0.29	12.3–12.8	2.0		
Jamaica	33	12.5 \pm 0.07	12.1–12.8	1.5		
Dominican Republic	11	12.5 \pm 0.09	12.3–12.7	1.2		
Bahamas	2	13.7	13.6–13.8			
<i>Zygomatic breadth</i>						
Male						
Bahamas	6	7.1 \pm 0.08	7.0–7.3	1.4	56.297	I
Dominican Republic	30	6.5 \pm 0.05	6.1–6.7	2.1	2.76	I
Jamaica	13	6.5 \pm 0.04	6.3–6.6	1.2		I
Old Providence	8	6.4 \pm 0.09	6.3–6.7	2.0		I
Cuba	2	6.7	6.6–6.7			
Female						
Old Providence	3	6.5 \pm 0.07	6.5–6.6	0.9	0.416	ns
Dominican Republic	10	6.5 \pm 0.10	6.1–6.6	2.4		
Cuba	4	6.5 \pm 0.16	6.3–6.7	2.5		
Jamaica	34	6.5 \pm 0.05	6.0–6.7	2.1		
Bahamas	2	7.3	7.2–7.4			

Table 2.—Continued.

Sex and locality	N	Mean \pm 2 SE	Range	CV	F _s F	Results SS-STP
<i>Postorbital breadth</i>						
Male						
Bahamas	6	2.8 \pm 0.04	2.8–2.9	1.8	11.259	I
Dominican Republic	32	2.7 \pm 0.03	2.5–2.9	3.3	2.76	I
Jamaica	16	2.6 \pm 0.05	2.5–2.9	3.8		I
Old Providence	8	2.6 \pm 0.05	2.5–2.7	2.5		I
Cuba	2	2.8	2.7–2.8			
Female						
Dominican Republic	11	2.7 \pm 0.06	2.6–2.9	3.8	1.944	ns
Jamaica	37	2.6 \pm 0.02	2.5–2.8	2.7		
Old Providence	3	2.6	2.6			
Cuba	5	2.6 \pm 0.10	2.4–2.7	4.2		
Bahamas	2	2.9	2.8–2.9			
<i>Breadth of braincase</i>						
Male						
Bahamas	6	6.4 \pm 0.06	6.3–6.5	1.2	21.145	I
Dominican Republic	32	6.0 \pm 0.05	5.7–6.3	2.4	2.76	I
Jamaica	16	6.0 \pm 0.06	5.8–6.2	2.1		I
Old Providence	8	5.8 \pm 0.08	5.7–6.0	2.0		I
Cuba	2	5.9	5.8–5.9			
Female						
Dominican Republic	11	6.0 \pm 0.07	5.8–6.2	2.0	1.613	ns
Jamaica	37	5.9 \pm 0.03	5.7–6.1	1.6		
Old Providence	3	5.9 \pm 0.07	5.8–5.9	1.0		
Cuba	4	5.9 \pm 0.17	5.7–6.1	3.0		
Bahamas	2	6.4	6.3–6.4			
<i>Mastoid breadth</i>						
Male						
Bahamas	5	6.9 \pm 0.09	6.8–7.0	1.5	42.536	I
Dominican Republic	32	6.4 \pm 0.04	6.2–6.6	1.9	2.76	I
Jamaica	12	6.3 \pm 0.05	6.2–6.4	1.4		I
Old Providence	3	6.2 \pm 0.12	6.1–6.3	1.6		I
Cuba	1	6.5				
Female						
Dominican Republic	10	6.3 \pm 0.06	6.2–6.5	1.6	0.331	ns
Cuba	4	6.3 \pm 0.08	6.2–6.4	1.3		
Jamaica	33	6.3 \pm 0.04	6.1–6.5	1.6		
Old Providence	2	6.3 \pm 0.10	6.2–6.3	1.1		
Bahamas	2	7.0	6.8–7.1			

Table 2.—*Continued.*

Sex and locality	N	Mean \pm 2 SE	Range	CV	F _s F	Results SS-STP
<i>Length of maxillary toothrow</i>						
Male						
Bahamas	6	6.6 \pm 0.11	6.4–6.8	2.1	81.235	I
Jamaica	15	5.9 \pm 0.05	5.7–6.1	1.6	2.76	I
Dominican Republic	31	5.9 \pm 0.04	5.6–6.1	1.9		I
Old Providence	8	5.8 \pm 0.05	5.7–5.9	1.3		I
Cuba	3	6.0	5.9–6.1			
Female						
Cuba	5	6.0 \pm 0.07	5.9–6.1	1.4	3.681	I
Dominican Republic	11	5.9 \pm 0.04	5.8–6.0	1.1	2.76	I
Jamaica	37	5.9 \pm 0.04	5.7–6.1	1.9		I
Old Providence	4	5.8 \pm 0.05	5.8–5.9	0.9		I
Bahamas	2	6.7	6.6–6.7			
<i>Breadth across upper molars</i>						
Male						
Bahamas	6	4.9 \pm 0.08	4.8–5.0	2.0	63.730	I
Dominican Republic	31	4.4 \pm 0.03	4.2–4.6	1.9	2.76	I
Old Providence	8	4.3 \pm 0.12	4.0–4.5	3.8		I
Jamaica	16	4.3 \pm 0.05	4.1–4.4	2.2		I
Cuba	3	4.5	4.5–4.6			
Female						
Dominican Republic	11	4.4 \pm 0.05	4.2–4.5	2.0	1.636	ns
Old Providence	3	4.4 \pm 0.13	4.3–4.5	2.6		
Cuba	5	4.3 \pm 0.16	4.1–4.5	4.2		
Jamaica	37	4.3 \pm 0.04	4.0–4.6	3.0		
Bahamas	2	4.9	4.9			
<i>Depth of braincase</i>						
Male						
Bahamas	6	5.1 \pm 0.08	5.0–5.3	2.0	3.819	I
Jamaica	16	5.0 \pm 0.06	4.8–5.2	2.5	2.76	I
Dominican Republic	32	5.0 \pm 0.07	4.7–6.0	4.2		I
Old Providence	6	4.8 \pm 0.08	4.7–5.0	2.0		I
Cuba	2	4.8	4.7–4.8			
Female						
Jamaica	37	5.0 \pm 0.03	4.8–5.2	1.9	9.470	I
Dominican Republic	11	4.8 \pm 0.06	4.7–5.0	1.9	2.76	I
Cuba	4	4.8 \pm 0.15	4.7–5.0	3.1		I
Old Providence	3	4.7 \pm 0.07	4.7–4.8	1.2		I
Bahamas	2	5.1	5.1			

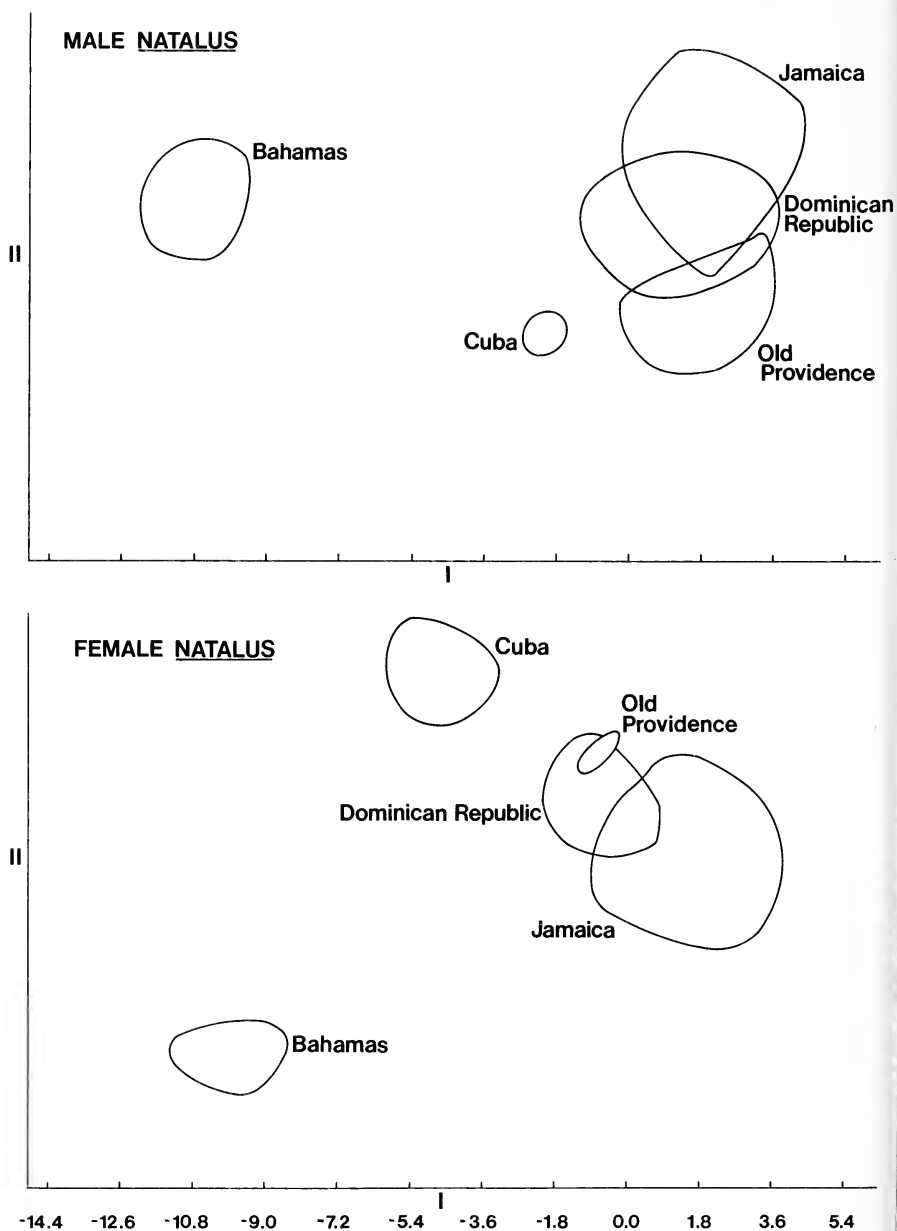


Fig. 1.—Two-dimensional projection of the first two canonical variates of male (upper) and female (lower) samples of the *Natalus micropus*-complex, based on a classification of variance-covariance among three external and nine cranial measurements.

Table 3.—*Variables used in discriminant function analysis of males and females of the Natalus micropus-complex. Characters are listed in order of their usefulness in distinguishing groups, with the character with the greatest between-groups variance and the least within-groups variance being selected first. The statistics are recalculated at each step.*

Step	Character	F-value	U-statistic
<i>Males</i>			
1)	Condylobasal length	102.20	0.0952
2)	Length of phalanx 1 (digit III)	7.49	0.0555
3)	Breadth across upper molars	5.27	0.0367
4)	Length of forearm	3.04	0.0281
5)	Depth of braincase	2.88	0.0217
6)	Mastoid breadth	2.32	0.0175
7)	Postorbital breadth	1.21	0.0154
8)	Length of maxillary toothrow	1.13	0.0137
9)	Length of metacarpal III	1.38	0.0119
10)	Zygomatic breadth	0.62	0.0110
11)	Breadth of braincase	0.88	0.0100
12)	Greatest length of skull	0.62	0.0093
<i>Females</i>			
1)	Length of maxillary toothrow	25.94	0.2881
2)	Length of forearm	23.53	0.0874
3)	Length of phalanx 1 (digit III)	6.79	0.0521
4)	Mastoid breadth	5.71	0.0328
5)	Condylobasal length	3.75	0.0235
6)	Greatest length of skull	2.94	0.0178
7)	Depth of braincase	4.86	0.0116
8)	Breadth of braincase	1.97	0.0095
9)	Length of metacarpal III	1.44	0.0081
10)	Zygomatic breadth	1.29	0.0070
11)	Postorbital breadth	0.66	0.0065
12)	Breadth across upper molars	0.45	0.0061

from Jamaica, whereas the samples averaged the same in the other five.

Multivariate Analyses.—Canonical analyses provides a procedure for graphically representing phenetic relationship among samples with the characters weighted by variance-covariance analysis. Examination of the two-dimensional plots of the male and female samples of the *micropus*-complex presented in Fig. 1 reveals two distinct groups well separated on the first variate. In the males, the Bahamas sample is found on the left side of the plot, whereas those from Jamaica, the Dominican Republic, Old Providence Island, and Cuba are grouped on the right. In this latter group, Cuba is found close to the other three samples but is separated from them on Variate I, whereas the other samples overlap. In the females, the sample from the Bahamas is found

Table 4.—*Classification matrix for male and female samples of the Natalus micropus-complex, based upon the discriminant functions of 12 morphometric characters. Values indicate the number of individuals classified into each group.*

Sample	Classification groups				
	1	2	3	4	5
<i>Males</i>					
1) Jamaica	8	1	0	1	0
2) Dominican Republic	2	27	0	0	0
3) Cuba	0	0	1	0	0
4) Old Providence	0	0	0	3	0
5) Bahamas	0	0	0	0	5
<i>Females</i>					
1) Jamaica	30	0	0	0	0
2) Dominican Republic	0	9	0	0	0
3) Cuba	0	0	4	0	0
4) Old Providence	0	1	0	1	0
5) Bahamas	0	0	0	0	2

at the bottom of the left side of the plot, and those from Jamaica, the Dominican Republic, Old Providence Island, and Cuba, diagonally opposite, are clustered higher at the right side of the plot. The sample from Cuba is found at the top middle of the plot on Variate I, separated from the cluster of samples from Jamaica, the Dominican Republic, and Old Providence Island. The sample from the Bahamas is widely separated from Cuba on Variate II.

The amount of total dispersion accounted for male and female samples of the *micropus*-complex, respectively, was 85.4 and 61.7% for Variate I, and 7.8 and 24.2% for Variate II. In Table 3, characters used in this analysis are listed from the most useful to the least useful in discriminating groups. Characters with high positive canonical coefficients for Variate I (values greater than 1.5) were, in decreasing order of values, depth of braincase for males, and length of forearm, and condylobasal length for females. Those with high negative values include, ordered as above, condylobasal length, breadth across upper molars, and mastoid breadth for males, and mastoid breadth, length of maxillary toothrow, and postorbital breadth for females. In Variate II, positive values of more than 1.5 were, in decreasing order of value, depth of braincase, length of maxillary toothrow, and zygomatic breadth for males, and mastoid breadth for females. The characters with high negative values were postorbital breadth, breadth across upper molars, and greatest length of skull for males, and breadth of braincase, zygomatic breadth, mastoid breadth, and condylobasal length for females.

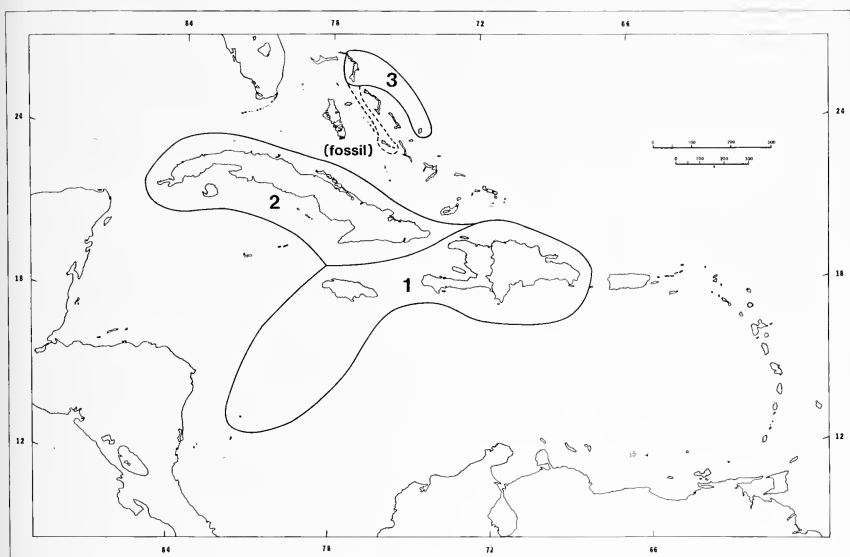


Fig. 2.—Map showing distribution of *Natalus micropus* and *N. tumidifrons*. 1) *N. m. micropus*; 2) *N. m. macer*; 3) *N. tumidifrons*.

A similar arrangement of the geographical relationship of the samples offered by the canonical analysis (Fig. 1) is suggested in the distribution of individuals by the classification matrix (Table 4). This analysis shows that of the individuals in the sample from Jamaica, two males are misclassified with specimens from the Dominican Republic and Old Providence, two males from the Dominican Republic are misclassified with the Jamaican sample, and a female from Old Providence is misclassified with the sample from the Dominican Republic. The remaining specimens including all the specimens from Cuba and the Bahamas involved in this analysis are classified in their proper group.

Taxonomic Conclusions

Based on our interpretations of the univariate and multivariate analyses, we consider that the *Natalus micropus*-complex represents two morphologically distinct species, *Natalus micropus* from Cuba, Jamaica, Hispaniola (Dominican Republic and Haiti), and Old Providence Island, and *N. tumidifrons* from the Bahama Islands. *Natalus tumidifrons* is clearly distinguishable from the several populations of *N. micropus* on the basis of larger size. In six characters for males and seven for females of the 12 characters studied, there was no overlap

between the two species in the range of measurements when compared by sex.

Natalus tumidifrons is considered to be monotypic, whereas two subspecies are recognized within *N. micropus*. *N. m. micropus* occurs on Jamaica, Old Providence Island, and Hispaniola and *N. m. macer* occurs on Cuba and the Isle of Pines (see discussion below for distinguishing characters).

SYSTEMATIC ACCOUNTS

Genus *Natalus* Gray

1838. *Natalus* Gray, Mag. Zool. Bot., 2:496, December.

Type species.—*Natalus stramineus*

Natalus tumidifrons Miller, 1903

1903. *Chilonatalus tumidifrons* Miller, Proc. Biol. Soc. Washington, 16:119, September 30.

1950. *Natalus (Chilonatalus) tumidifrons*, Dalquest, J. Mamm., 31:443, November 21.

1974. *Natalus micropus tumidifrons*, Varona, Acad. Cien. Cuba, p. 32.

Holotype.—Adult male, in alcohol with skull removed, USNM 122024, obtained near Sandy Point, Watling Island [=San Salvador Island], Bahamas, by J. H. Riley on 12 July 1903; original number 157.

Measurements of holotype.—Length of forearm, 33.5; length of metacarpal III, 32.8; length of phalanx 1 (digit III), 14.4; greatest length of skull, 15.4; condylobasal length, 13.6; zygomatic breadth, 7.2; postorbital breadth, 2.9; breadth of braincase, 6.3; mastoid breadth, 6.8; length of maxillary toothrow, 6.6; breadth across upper molars, 4.9; depth of braincase, 5.1.

Distribution.—Bahama Islands: Watling and Great Abaco islands (Fig. 2). Also known as fossil from Great Exuma (Koopman et al., 1957).

Diagnosis.—Distinguished by large cranial size from the closely related *N. micropus*.

Comparisons.—Skull and teeth are larger in *Natalus tumidifrons* than in *Natalus micropus*. Occurring allopatrically both species can be clearly separated by cranial measurements (Table 2). Comparing the sexes of the two species separately there is no overlap in the following measurements: greatest length of skull, condylobasal length, zygomatic breadth, breadth of braincase (females only), mastoid breadth, length of maxillary toothrow, and breadth across upper molars. Standard statistics are given in Table 2.

Remarks.—The relationship of the insular populations of the genus *Natalus*, and the differences found between *N. tumidifrons* and *N. micropus* suggest a pattern comparable to other West Indian chiropteran taxa. Similar cases are represented by the genus *Pteronotus* with

the sympatric species *P. macleayii* and *P. quadridens* in the Greater Antilles (Smith, 1972) and by the two allopatric species of the genus *Brachyphylla* (Swanepoel and Genoways, 1978) in the Greater Antilles, Lesser Antilles, and the Bahamas.

Specimens examined (59).—WATLING ISLAND [=San Salvador Is.]: N. Victoria Hill, 2 (USNM); no specific locality, 7 (USNM). GREAT ABACO ISLAND: no specific locality, 3 (2 FMNH, 1 AMNH); Marsh Harbor, Israel's Point, 47 (MCZ).

Natalus micropus

Distribution.—This species occurs on Cuba, Isle of Pines, Hispaniola (Dominican Republic), Jamaica, and Old Providence Island (Fig. 2).

Diagnosis.—Smaller cranially than the closely related *Natalus tumidifrons*, making it one of the smallest species of the genus.

Comparisons.—See account for *Natalus tumidifrons*.

Remarks.—Varona (1974) and Hall (1981) have proposed that *brevimanus* from Old Providence Island and *macer* from Cuba and Isle of Pines represent only subspecies of *micropus*, which was originally described from Jamaica. A univariate comparison (Table 2) of these geographical populations, including a sample of the previously unreported population from the Dominican Republic, indicates that the population from Cuba and Isle of Pines averaged larger than the samples from Jamaica, Dominican Republic, and Old Providence Island in length of phalanx 1 (digit III), length of maxillary toothrow, and condylobasal length. Although the males available from Cuba and Isle of Pines were not enough to be entered in the analyses, the means in the female sample averaged smaller than the other three populations in length of forearm, length of metacarpal III, postorbital breadth, and breadth of braincase. The multivariate analyses (Fig. 1) showed the samples from Jamaica, Dominican Republic, and Old Providence Island clustered at the right side of the plot separated from the population from Cuba and Isle of Pines on Variate I in both males and females.

In order to better understand the relationship of the populations of *Natalus micropus*, additional multivariate analyses of these populations were performed excluding *Natalus tumidifrons* from the Bahamas. This showed the sample from Cuba well separated from the other populations on Variate I in the females and on Variate I and II in the males. The populations from Jamaica, Dominican Republic, and Old Providence Island were grouped together and overlapping, with the Dominican Republic intermediate. The classification matrix indicated that 100% of the individuals from Cuba (both sexes) could be correctly identified using only two characters—length of forearm and length of phalanx 1 (digit III).

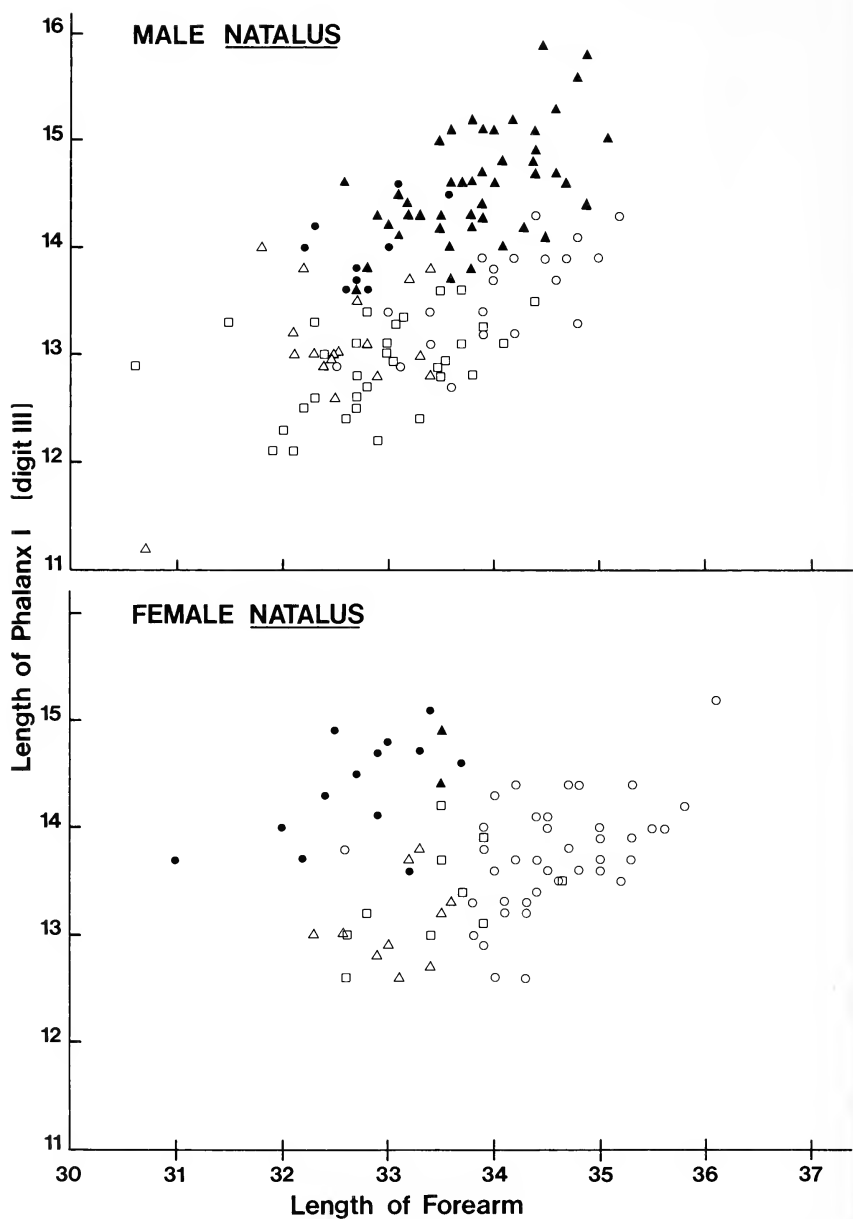


Fig. 3.—Bivariate plot of values of length of forearm and length of phalanx I (digit III) to show the relationship of samples of the *Natalus micropus*-complex. Open circles are specimens from Jamaica; closed circles from Cuba; open triangles from Old Providence Island; closed triangles from the Bahamas; open squares from Dominican Republic.

Because of the results of the classification analyses, we prepared a bivariate plot of length of forearm and length of phalanx 1 (digit III) of all samples, to determine the range of variation among them. Using only these two external measurements allowed us to include data for many specimens not used in the multivariate analyses. The bivariate plots (Fig. 3) show the Cuban samples of males and females are distinguishable from the samples from Jamaica, Dominican Republic, and Old Providence Island on the basis of these two characteristics. The specimens of *Natalus micropus* from Cuba have a longer phalanx 1 (digit III) and relatively shorter forearm than other populations of *Natalus micropus*. In these characteristics, the Cuban population is more similar to *N. tumidifrons* than other populations of *N. micropus*. Based on results of this analysis of geographic variation in *Natalus micropus*, we believe that the relationship among these populations is best represented by considering them to be two subspecies.

Natalus micropus micropus Dobson, 1880

1880. *Natalus micropus* Dobson, Proc. Zool. Soc. London, p. 443, October.
1898. *Natalus (Chilonatalus) brevimanus* Miller, Proc. Acad. Nat. Sci. Philadelphia, 50:328, July.
1907. *Chilonatalus brevimanus*, Elliot, Field Columbian Mus., Zool. Ser., 7:525.
1907. *Chilonatalus micropus*, Miller, Bull. U.S. Nat. Mus., 57:185.
1907. *Chilonatalus brevimanus*, Miller, Bull. U.S. Nat. Mus., 57:185.
1950. *Natalus (Chilonatalus) micropus*, Dalquest, J. Mamm., 31:443, November 21.
1950. *Natalus (Chilonatalus) brevimanus*, Dalquest, J. Mamm., 31:443, November 21.
1974. *Natalus micropus brevimanus*, Varona, Acad. Cien. Cuba, p. 31.
1974. *Natalus micropus micropus*, Varona, Acad. Cien. Cuba, p. 32.

Holotype.—Adult male, skin and skull, BMNH 80.12.14.1 from Kingston, Jamaica, obtained by G. E. Dobson.

Measurements of holotype.—Length of forearm, 33.5; greatest length of skull, 14.5; condylobasal length, 13.3; zygomatic breadth, 2.6; mastoid breadth, 6.3; length of maxillary toothrow, 6.1; breadth across upper molars, 4.4.

Distribution.—Jamaica, Hispaniola (Dominican Republic), and Old Providence Island (Fig. 2).

Comparisons.—*Natalus micropus micropus* is distinguishable from *Natalus micropus macer* by size differences in external measurements. In a bivariate plot (Fig. 3) male and female samples of *micropus* are separable from male and female samples of *macer* by a combination of the length of forearm (shorter) and length of phalanx 1 (digit III) (longer).

Remarks.—The population described as *brevimanus* (Miller, 1898) was considered a distinct species for a long time until it was recently reduced to a subspecies of *N. micropus* by Varona (1974). It is worthy of note that when this population was originally reported from Old

Providence Island, it was referred to *N. micropus* (Allen, 1890). Based upon our study, we do not believe that this population should be given subspecific designation. Individuals from Old Providence Island averaged smaller than others in many measurements, but the range of measurements overlapped with those from Jamaica and particularly Hispaniola.

The specimens reported herein from the Dominican Republic are the first known from the island of Hispaniola. In many characteristics the population was intermediate to, and overlapping with, those from Jamaica and Old Providence Island. The finding of *Natalus micropus micropus* on the island of Hispaniola gives additional evidence of the relative close faunal relationship of this island and Jamaica.

Specimens examined (142).—DOMINICAN REPUBLIC: Cueva No. 2 Los Patos, Barahona Province, 30 (UPS); Cueva Vicente, Samana Province, 14 (4 AMNH, 10 UPS). JAMAICA: Balaclava, 3 (AMNH); Kingston, 1 (BMNH); Moneague, 1 (USNM); Montego Bay, 2 (USNM); Port Antonio, 5 (USNM); St. Clair Cave, 2 mi S Ewarton, St. Catherine Parish, 53 (33 CM, 19 TTU, 1 AMNH); no specific locality, 2 (USNM). OLD PROVIDENCE ISLAND: no specific locality, 31 (28 USNM, 2 FMNH, 1 AMNH).

Natalus micropus macer Miller, 1914

1914. *Chilonatalus macer* Miller, Proc. Biol. Soc. Washington, 27:225, December.

1950. *Natalus (Chilonatalus) macer*, Dalquest, J. Mamm., 31:443, November 21.

1970. *Natalus micropus macer*, Viña Bayes and Deas Diaz, Acad. Cien. Cuba, Ser. Espinol. Carsol., 24:7.

1974. *Natalus micropus macer*, Varona, Acad. Cien. Cuba p. 32.

Holotype.—Adult female, in alcohol with skull removed, USNM 113724 from Cueva de la Majana, Baracoa, Cuba, obtained by William Palmer on 6 February 1902; original No. 699.

Measurements of holotype.—Length of forearm, 32.8; length of metacarpal III, 31.0; greatest length of skull, 14.3; condylobasal length, 12.8; zygomatic breadth, 6.7; postorbital breadth, 2.6; breadth of braincase, 6.1; mastoid breadth, 6.2; length of maxillary toothrow, 6.1; breadth across upper molars, 4.2; depth of braincase, 4.9.

Distribution.—Cuba and Isla de Pinos (Fig. 2).

Comparisons.—See account for *Natalus micropus micropus*.

Remarks.—When the population from Cuba was first reported, it was regarded as *N. micropus* (Miller, 1904; Allen, 1911), but was later named as a distinct species (Miller, 1914). More recently, this population was considered a subspecies of *N. micropus*. The current study supports this status proposed by Viña Bayes and Deas Diaz (1970) and Varona (1974) and adopted by later authors (Silva, 1979; Hall, 1981).

Specimens examined (28).—CUBA: Cueva de los Paredones, Ceiba del Agua, La Habana Province, 1 (AMNH); Finca Quinones, Pinar del Rio Province, 1 (MCZ); San Vicente, Pinar del Rio Province, 5 (4 AS, 1 AMNH); Cueva de la Majana, Baracoa,

Oriente Province, 6 (2 USNM, 2 MCZ, 2 AMNH); Guantanamo, Oriente Province, 7 (USNM). ISLA DE PINOS: Cueva de Punta Brava, 8 (4 FMNH, 4 AMNH).

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ARTICLE 3

REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 1. INTRODUCTION AND MULTITUBERCULATA

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ABSTRACT

A P_4 and two molars of the neoplagiaulacid *Ectypodus* sp. cf. *E. childei* provide the first known occurrence of multituberculates in the Wind River Formation and in the late Wasatchian. The multituberculate localities (Deadman Butte and Viverravus) occur in sediments in the Deadman Butte area of the Wind River Basin and have also yielded a Lostcabinian mammalian fauna. These sediments represent a hitherto unrecognized lithological sequence of the Wind River Formation that is time equivalent to part of the Lysite and Lost Cabin Members.

INTRODUCTION: HISTORY OF INVESTIGATION

Fossil vertebrates were first found in sediments of the Wind River Formation in 1880 by Jacob L. Wortman, who was working in the northeastern part of the Wind River Basin for E. D. Cope (1880; see Tourtelot, 1948). Wortman's discovery of early Eocene fossil vertebrates confirmed the correlation of Wind River sediments with those of the Wasatch Eocene of northwestern New Mexico and southwestern Wyoming proposed on lithological grounds in 1878 by F. V. Hayden, who first described the "Wind River deposits" or "Wind River group" (Meek and Hayden, 1861).

Wortman made additional collections in the Wind River Formation

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Submitted 19 May 1981.

in 1891 and 1896, but it was not until the early 1900's that Frederick B. Loomis of Amherst College and Walter Granger of the American Museum of Natural History made stratigraphically controlled collections of fossil vertebrates from these deposits. This work formed part of the nucleus for a series of papers that reviewed the systematics of many groups of North American early Cenozoic fossil vertebrates (Granger, 1908, 1910, 1915; Loomis, 1905, 1906, 1907; Matthew, 1910, 1915*a*, 1915*b*, 1915*c*, 1918; Matthew and Granger, 1915; Sinclair, 1914; Osborn and Wortman, 1892; Wortman, 1903, 1904) and resulted in the recognition of two distinct early Eocene faunal and lithological horizons. Sinclair and Granger (1911:104) named the lower horizon the "Lysite formation" and the upper horizon the "Lost Cabin formation." The faunal distinction was based on the absence of the perissodactyl genera *Lambdotherium*, *Eotitanops*, and *Systemodon* (= *Homogalax*) in the Lysite Formation and the presence of *Lambdotherium* and *Eotitanops* as well as absence of *Systemodon* in the Lost Cabin formation. Sinclair and Granger (1911:4) also summarized the geological differences between the two horizons. The Lysite formation sediments "comprise yellow, gray and brick-red shales or clays with interstratified buff, pale blue, yellow-brown and gray sandstones, dipping at a low angle away from the Bridger Range and passing beneath the bluish shales and gray and yellow sandstone with *Lambdotherium* along Alkali Creek [lower boundary of the Lost Cabin formation]. These, in turn, lie *below* the red and blue banded beds, also with *Lambdotherium*, forming the divide between Alkali and Poison Creeks north of Moneta. Throughout there is conformable superposition" (original emphasis in italics). It is evident from their discussion that, within the Lost Cabin formation, Sinclair and Granger recognized a lower unit dominated by gray-colored lithology as well as an upper unit dominated by variegated-colored lithology, each of which contained *Lambdotherium*.

After 1918, collecting of fossil vertebrates from the Wind River Formation continued on almost a year by year basis (see Tourtelot, 1948; Guthrie, 1967, 1971). In 1941, Wood et al. indicated that the "Lysite member (or formation)" and the "Lost Cabin member (or formation)" were "valid, mapable lithologic unit(s)" of the "Wind River formation (or group)," but did not specifically state that these beds were exactly coincident with the faunal zones proposed earlier by Osborn (1929) and Wilmarth (1938). In a review of the fauna of the Wind River Formation Van Houten (1945) used the terms "Lysite" and "Lost Cabin" to refer to names of "beds" and "faunas." Tourtelot (1946, 1948, 1953), following Sinclair and Granger (1911), concluded that both the Lysite and Lost Cabin sediments should rank as members of the Wind

River Formation, and used the following criteria to distinguish between them: In the Lysite Member "1. Conglomerates . . . consist chiefly of debris from post-Cambrian Paleozoic rocks and locally contain some Mesozoic rock fragments. Pre-Cambrian rock fragments occur sporadically near the top of the member. 2. Brick-red and orange-red are the predominant colors in the variegated beds of the Lysite; violet shades are rare. 3. Variegated beds of the Lysite grade laterally into gray and drab-colored, fine-grained beds. 4. Sandstones contain only a little white mica and almost no black mica" (Tourtelot, 1948:57).

In the Lost Cabin Member "1. Conglomerates consist of debris from pre-Cambrian and Cambrian rocks. 2. The most prevalent red colors in the variegated beds are violet in shade; purple and purplish-red colors are common. 3. The variegated beds grade laterally into conspicuous gray and grayish-green beds of similar lithology. 4. Sandstones contain abundant black mica and some feldspar grains" (Tourtelot, 1948:60).

Subsequent workers in the Wind River Formation have recognized Tourtelot's distinctions between the Lysite and Lost Cabin Members (for example, Woodward, 1957; Keefer, 1965a; Guthrie, 1967, 1971; Love, 1978; and this paper). Lewis and Gazin (*in* Tourtelot, 1953) and Van Houten (1945) also confirmed the faunal distinctions established between the two members by Sinclair and Granger (1911). Kelley and Wood (1954) added new taxa to the mammalian fauna of the Lysite Member and discussed the utility of these taxa in biostratigraphic correlation. Keefer (1965a, 1965b, 1970) described the stratigraphy and structural geology of the Wind River Basin and Guthrie (1967, 1971) reconfirmed the distinct nature of the faunas from the Lysite and Lost Cabin Members. He also noted that he had recovered a tooth fragment of *Lambdotherium* from "the upper part of the beds of Lysite lithology" (Guthrie, 1967:4).

Although no systematic review of the faunas from the Wind River Formation has been published since Guthrie's review, intensive paleontological collecting has proceeded in the Badwater Creek area of the Wind River Basin from 1968 to the present. Carnegie Museum of Natural History field parties led by Craig C. Black, Mary R. Dawson and, most recently, the junior author, have recovered the largest known assemblage of fossil vertebrates from the Wind River Formation, as well as significant collections from the Paleocene Fort Union Formation (Krishtalka et al., 1975), the series of Uintan and Duchesnean localities in the Hendry Ranch deposits (=Wagon Bed Formation, J. D. Love, personal communication, 1980; Lageson, 1980; Black and Dawson, 1966, and other papers in this series) and the Oligocene White River Formation (Setoguchi, 1978). This paper is the first part

of a comprehensive review of the geology, paleontology, and paleoecology of the Wind River Formation, and deals exclusively with a preliminary geological and paleontological assessment of the deposits in the Deadman Butte area as well as the systematics of the multiberculate remains recovered from the Deadman Butte and Viverravus localities. The geology of the Wind River Formation in the Badwater Creek and surrounding areas is currently under study (William W. Korth, University of Pittsburgh, in preparation) as are the systematics, relationships, and biostratigraphic implications of taxa recovered from these deposits.

PRELIMINARY GEOLOGY OF THE WIND RIVER FORMATION, DEADMAN BUTTE AREA

The Deadman Butte area is defined as the area of Wind River Formation exposures to the west of E-K Creek in Section 22, Township 38N, Range 87W, Natrona County, Wyoming. Sediments of the Wind River Formation are well exposed on both sides of a ridge that extends to the south into Section 34, Township 38N, Range 87W. These exposures lie in the extreme northeastern corner of the Wind River Basin (Fig. 1, see also Plate 1, Keefer, 1965*a*). Sediments of the Wind River Formation in this area strike nearly parallel to Dry Fork Fault (Tourtelot, 1953). These sediments are flat lying at the Deadman Butte (UCM V-80062) and Viverravus (UCM V-81008) localities. However, a monocline is developed to the south of these localities where dip is 10° South. En echelon faults of minor displacement (less than 10 m) trend parallel to Dry Fork Fault along the southern margin of the monocline. Stratigraphic relations of the Lysite and Lost Cabin Members of the Wind River Formation recognized in the Badwater area (Granger, 1910; Sinclair and Granger, 1911; Tourtelot, 1948; Keefer, 1965*a*; Love, 1978), cannot be applied with certainty to the sediments of the Wind River Formation in the Deadman Butte area. Tourtelot (1953) and Woodward (1957) did not distinguish the two members in this area, nor did they describe in detail the lithology of the sediments. Both authors, however, found fossil vertebrates near what is here named the Deadman Butte locality. Although Keefer (1965*a*) mapped the Lysite and Lost Cabin Members on the western flank of the Casper Arch and accepted Tourtelot's (1953) mapping of these members in the Badwater area, he did not map the intervening sediments in the Deadman Butte area and along Red Creek.

Geologic work conducted during 1979, 1980, and 1981 has clarified the relative stratigraphic positions of the Deadman Butte and Viverravus localities and the stratigraphic and lithologic relations of sediments of the Wind River Formation in the Deadman Butte area. Two

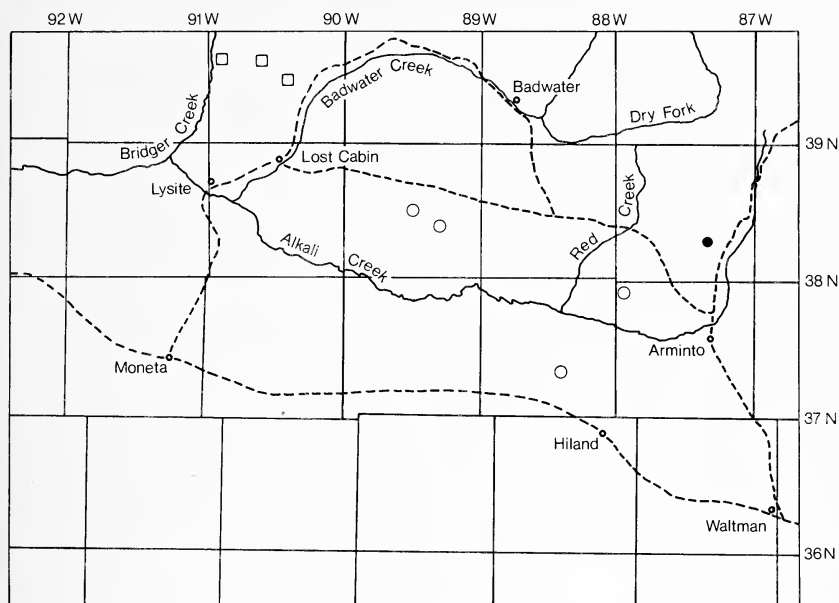


Fig. 1.—Sketch map of type area of the Lysite and Lost Cabin Members, Wind River Formation, Wyoming, showing localities in the Lysite Member (open squares), Lost Cabin Member (open circles), and the Deadman Butte and Viverravus localities (black circle). Modified from Guthrie (1971:49, Fig. 1).

lithostratigraphic sequences can be mapped in this area: 1) a lower gray sequence characterized by tuffaceous medium light gray to light olive brown mudstones and claystones and yellowish gray to grayish yellow sandstones that contain lenticular well-defined conglomerates derived from predominantly Mesozoic rocks; and 2) an overlying variegated sequence characterized by alternating red and drab mudstones, yellow-brown shoestring channel sandstones, and conglomerates with clasts derived from Precambrian rocks. The lower gray sequence, varying in thickness from a wedge edge to 120 feet (37 m), cannot be assigned to any member of the Wind River Formation; it differs lithologically from the gray unit of the Lost Cabin Member of Sinclair and Granger (1911) in the presence of predominantly Mesozoic as opposed to Precambrian clasts in conglomerates and sandstones and in its tuffaceous nature. This lower gray sequence differs from the Lysite Member in these attributes and in the lack of any red colored sediments. The lower gray sequence was deposited unconformably on top of Me-

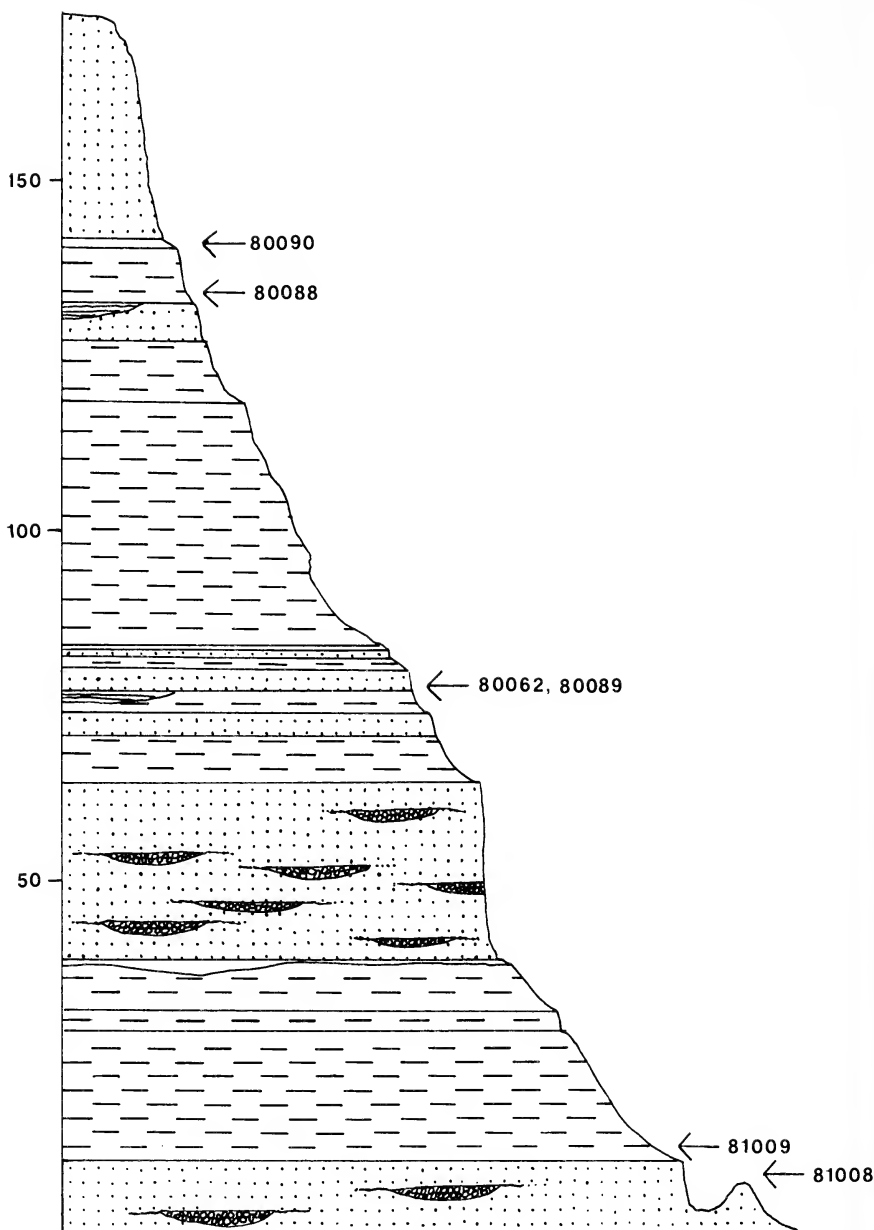


Fig. 2.—Composite columnar section showing stratigraphic positions of the Deadman Butte (UCM V-80062), *Viverravus* (UCM V-81008), and other localities in the Deadman Butte area. Note that uppermost sandstone is first sandstone of Lost Cabin Member

sozoic rocks (Chugwater Group, Sundance Formation, Morrison and Cloverly Formations undivided, Thermopolis Shale and Mowry Shale) from which many of the clasts in the lower gray sequence were derived. Several exposures of Mesozoic rocks are completely surrounded by sediments of the lower gray sequence indicating topographic complexity during time of deposition. This lower gray sequence is probably stratigraphically equivalent to the variegated sequence of beds in the type area of the Lost Cabin Member near Buck Spring at Guthrie's Locality 3 (Sinclair and Granger, 1911; Guthrie, 1971). Sediments of the lower gray sequence represent a mountainward facies of the Wind River Formation that was developed from nearby Mesozoic exposures, whereas penecontemporaneous Lost Cabin Member sediments represent a basinward facies developed on broad floodplains from distant Precambrian exposures. On these bases as well as other lithological criteria the lower gray sequence of the Deadman Butte area could be defined as a new member of the Wind River Formation.

The variegated sequence in the Deadman Butte area, approximately 200 feet (61 m) thick, can be assigned to the Lost Cabin Member according to Tourtelot's (1948; see above) lithological criteria, but may be younger than the Lost Cabin Member in the type area (Stucky, unpublished data). As such, the Lost Cabin Member in the type area, the lower gray sequence in the Deadman Butte area, and the upper part of the Lysite Member (see Guthrie, 1967) may be time equivalent, and appear to represent sediments derived from different source areas deposited in an area of early Eocene topographic variability along the front of the Bighorn and Owl Creek Mountains.

The Deadman Butte (UCM V-80062) and Viverravus (UCM V-81008) localities differ in stratigraphic position but are nearly identical in lithology (Fig. 2). Both localities preserve a late Wasatchian fauna as indicated by the presence of *Lambothrium popoagicum* at each locality (Table 1). The Deadman Butte and Viverravus localities lie 62 feet (19 m) and 132 feet (38 m), respectively, below the lowermost sandstone of Lost Cabin Member lithology (see Fig. 2). Both localities are developed in yellowish gray to grayish yellow well-sorted fine to medium grained quartz arenites that are typical of the lower gray sequence. These sandstones are indurated and vertically weathering. Lenticular conglomerates with clasts derived from Mesozoic rocks are

←

aspect (sensu Tourtelot, 1948, see text). Vertical scale in feet. Key to lithologies of stratigraphic horizons: small circles indicate conglomerates; dots indicate sandstones; dashed lines indicate mudstones and siltstones; horizontal lines indicate carbonaceous shales; and blank horizons indicate claystones.

Table 1.—*Preliminary mammalian faunal list, Deadman Butte (UCM V-80062) and Viverravus (UCM V-81008) localities, Natrona County, Wyoming.*

Taxa	UCM V-80062	UCM V-81008
Multituberculata		
<i>Ectypodus</i> sp. cf. <i>E. childei</i>	X	X
Marsupicarnivora		
<i>Peratherium comstocki</i>	X	
<i>Peratherium</i> sp.	X	X
Proteutheria		
<i>Palaeoryctid</i> sp.	X	
<i>Didelphodus</i> sp.	X	
<i>Palaeictops</i> sp.	X	
<i>Apatemys</i> sp.	X	
Insectivora		
<i>Scenopagus edenensis</i>	X	X
<i>Scenopagus priscus</i>	X	
<i>Macrocranium</i> sp.	X	
<i>Talpavus</i> sp.	X	
<i>Nyctitherium</i> sp.	X	
<i>Centetodon</i> sp.	X	
Chiroptera		
Chiropteran sp.		X
Primates		
<i>Phenacolemur</i> sp.	X	X
<i>Microsyops</i> sp.	X	X
cf. <i>Niptomomys</i> sp.	X	
<i>Pelycodus</i> sp.	X	X
<i>Absarokius</i> sp.	X	
<i>Shoshonius</i> sp.	X	
<i>Loveina</i> sp.	X	X
Carnivora		
<i>Viverravus</i> sp. A (small)		X
<i>Viverravus</i> sp. B (large)		X
Miacid sp.	X	X
Creodonta		
unidentified sp.	X	
Tillodontia		
<i>Esthonyx</i> sp.	X	
Condylarthra		
<i>Hyopsodus</i> sp.	X	X
<i>Phenacodus</i> sp. A (small)	X	X
<i>Phenacodus</i> sp. B (large)	X	X

Table 1.—Continued.

Taxa	UCM V-80062	UCM V-81008
Pantodonta		
<i>Coryphodon</i> sp.		X
Perissodactyla		
<i>Hyracotherium</i> sp.	X	X
<i>Lambdotherium popoagicum</i>	X	X
<i>Heptodon</i> sp.	X	
<i>Selenaletes</i> sp.	X	
Artiodactyla		
<i>Diacodexis</i> sp.	X	X
cf. <i>Bunophorus</i> sp.	X	X
Rodentia*		
Ischyromyidae sps.	X	X
Sciuravidae sps.	X	X
<i>Paramys excavatus</i>	X	
<i>Paramys copei</i>	X	
" <i>Paramys</i> " <i>francesi</i>	X	
<i>Microparamys</i> sp.	X	
" <i>Mysops</i> " <i>kalicola</i>	X	
<i>Knightomys depressus</i>	X	
<i>Knightomys huerfanensis</i>	X	
<i>Pauromys</i> sp.	X	

* Rodents from the Deadman Butte locality were identified by William W. Korth of the Carnegie Museum of Natural History (personal communication, 1981).

enclosed within the sandstones. Lower contacts of these fossiliferous horizons are not exposed at either locality, however, upper contacts with mudstones are sharp. Sediments at the Viverravus locality were apparently subaerially exposed, as the upper part of the fossiliferous sandstone unit contains rhizoliths and pedotubules that resemble invertebrate burrows. These sedimentary structures are not preserved at the Deadman Butte locality.

Fossil vertebrates are randomly distributed throughout the sandstone bodies, but are less common in conglomerates. The most common elements are isolated teeth of mammals. Although data is limited, observations of *in situ* individual bones indicates that the probability of nearest neighbor bone element and taxa are equal to their frequencies of occurrence in the entire bone assemblage; no elements of the same individual are apparently associated. Most likely, the fossil assemblages were fluvially transported prior to burial in a stream system with high variation in stream competence as indicated by rock frag-

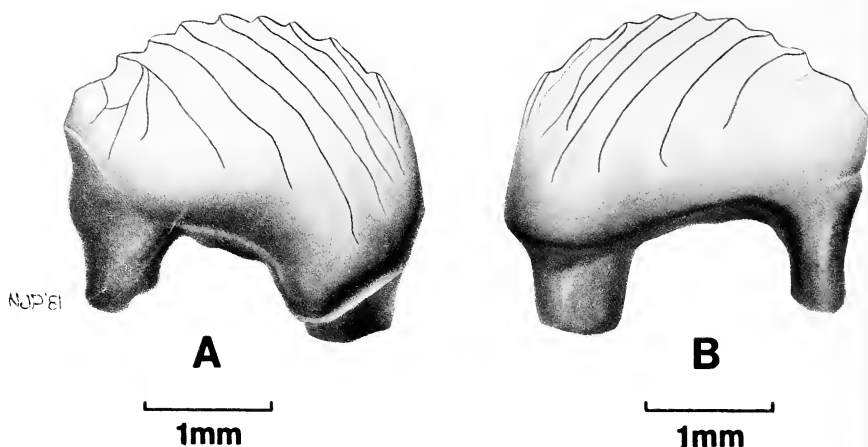


Fig. 3.—Labial (A) and lingual (B) views of UCM 46256, RP₄ of *Ectypodus* sp. cf. *E. childei*, from the late Wasatchian Viverravus locality, Wind River Formation, Wyoming.

ment size and size of individual bone elements (small rodent to large ungulate sized teeth). Fossils were recovered from each locality by surface prospecting and underwater screen washing (minimum Tylor screen size 35).

SYSTEMATICS

Order Multituberculata

Suborder Ptilodontoidea

Family Neoplagiaulacidae Ameghino, 1890

Eocene neoplagiaulacids are known in North America from the early Wasatchian of Wyoming, Colorado, and North Dakota (McKenna, 1960; Delson, 1971; West, 1973; Bown, 1979; Krishtalka, 1982; Krause, 1982), three Bridgerian and early Uintan localities (M. C. McKenna, J. Eaton, personal communication, 1979), and from late Uintan and Duchesnean sediments of Wyoming and Montana (Sloan, 1966; Krishtalka and Black, 1975). Described species include *Ectypodus tardus*, *Ectypodus* sp. cf. *E. childei*, *Parectypodus simpsoni*, *Parectypodus* n. sp. (Wasatchian), and *Ectypodus lovei* and *Ectypodus* sp. (late Uintan-Duchesnean), two species that also occur in Chadronian deposits and comprise the youngest known record of multituberculates (Krishtalka et al., 1982). The taxonomic affinities of the Bridgerian-early Uintan material is currently under study. If middle and late Clarkforkian records represent Eocene occurrences (Krause, 1980), *Parectypodus laytoni* and *Ectypodus powelli* should be added to this



Fig. 4.—Occlusal view of UCM 44565, LM₁ of *Ectypodus* sp. cf. *E. childei*, from the late Wasatchian Deadman Butte locality, Wind River Formation, Wyoming.

summary. *E. powelli* may (Krishtalka, 1982) or may not (Krause, 1980, 1982) be conspecific with *E. tardus*. The Wasatchian neoplagiaulacid taxa *Parectypodus* n. sp. and *Ectypodus* sp. cf. *E. childei* mentioned above are currently being described by D. W. Krause (1982) in a review of Wasatchian multituberculates. *E. childei* has recently been recognized (Godinot, 1981) as a senior synonym of *Charlesmooria childei* Kuhne, 1969, from the Wasatchian Abbey Wood locality, England, an action with which Krishtalka (1982) and Krause (1982) concur.

All measurements listed below are in millimeters.

Ectypodus Matthew and Granger, 1921

Ectypodus sp. cf. *E. childei*

(Figs. 3, 4, 5)

Material.—UCM (University of Colorado Museum) 46256, P₄; UCM 44565, M₁; UCM 44566, M₂.

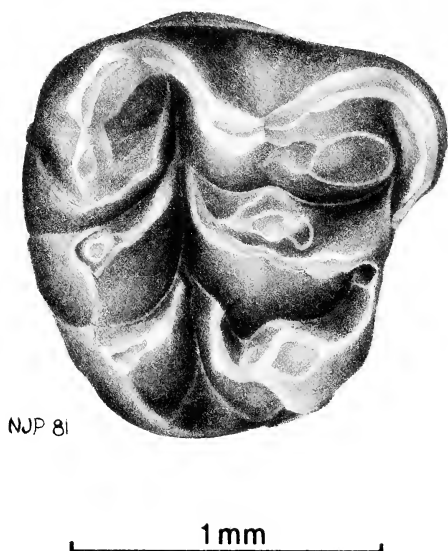


Fig. 5.—Occlusal view of UCM 44566, LM² of *Ectypodus* sp. cf. *E. childei*, from the late Wasatchian Deadman Butte locality, Wind River Formation, Wyoming.

Localities.—UCM locality 80062 (Deadman Butte) and 81008 (Viverravus), Wind River Formation, Wyoming.

Description.—P₄ [L (length) = 3.1] has nine serrations, of which the third is highest above the line for standard length. The relative height of the first serration—a diagnostic feature among neoplagiaulacids (Sloan, 1966; Krause, 1982; Krishtalka, 1982)—is 0.41. In labial profile the blade is higher anteriorly than posteriorly and is convex from the first to sixth serrations and more nearly straight from the latter to the last serration. The serrations become progressively more robust posteriorly; the last serration is especially large. The anterior edge of the blade between the anterobasal concavity and the first serration is straight, except for a slight flexure at a point one-third of the distance below the first serration. There is no appreciable overhang of enamel above the anterior root and the anterobasal concavity is extremely shallow. The anterior root bears a faint vertical groove on its anterior face. Each of the first eight serrations gives rise to a labial ridge, of which the second is weakest, and the sixth, longest. Two short posteroventral ridges arise from the eighth serration, and one from the last serration. These end in an area of wrinkled enamel above the posterolabial ledge. Lingually, the ridges from the first, and fourth to eighth serrations are strong, whereas that from the third is weak, and the one from the second is barely discernable. There are no discrete lingual posteroventral ridges, although the enamel is slightly wrinkled below the last serration.

The M₁ [L = 1.75; W (width) = 0.9] has a cusp formula of 6:4. The crown is rectangular in occlusal outline with slightly convex external and internal margins that diverge posteriorly to the level of the fifth external cusp. At this point the crown is widest and the external margin begins to curve posterointernally. The external row of cusps extends posteriorly beyond the internal one, so that the posterior margin of the crown is oblique. The first external cusp is small and conical, the second is larger and semi-pyramidal,

and the apices of both cusps point vertically. The remaining four external cusps are larger, subcrescentic, with apices directed posteriorly. The third cusp is slightly taller than the subequal fourth and fifth; the bases of the third and fourth cusps are longer than that of the fifth, but shorter than that of the sixth. The sixth external cusp appears structurally to be formed by the union of two cusps; its external face is smooth and long, but its internal face is divided by a deep vertical excavation that extends dorsally and faintly interrupts the elongate occlusal crest of the cusp into barely perceptible apices. In medial view then, the sixth cusp consists of an anterior cusp with a posteriorly directed apex and a lower posterior cusp with an anteriorly directed apex.

The first internal cusp on the M_1 is small and conical, whereas the remaining three are subcrescentic. A cline from the second to fourth internal cusps involves larger size, longer anterior slope, a more posteriorly directed apex and a deeper vertical groove on the medial face of each cusp. In occlusal view the first two cusps of each row are opposite one another, the third and fourth external cusps are opposite the third internal one, and the fifth external cusp is opposite the last internal one.

The M^2 ($L = 1.3$; $W = 1.3$; cusp formula 1:3:3) is triangular in occlusal view and moderately worn. The single anteroexternal cusp is small and ledge-like, whereas the medial and internal cusps are subcrescentic. The second cusp in the middle row is larger than the other two, and the three internal cusps are progressively smaller posteriorly.

Discussion.—In size, lateral profile, and relative height of the first serration the P_4 is identical to those of *Ectypodus* sp. cf. *E. childei* that Krause (1982) has identified in the collections from the early Wasatchian Despair Quarry, Four Mile Creek area, Colorado. Because of the small sample size, Krause (1982) refrained from referring the Four Mile material to *E. childei*, an action considered prudent and followed here for the P_4 from Viverravus locality and the two molars from the Deadman Butte locality. Godinot (1981) was similarly cautious in referring fragmentary material from the early Eocene of Rians, France to *Ectypodus* aff. *childei*.

UCM 46256 has nine serrations, whereas the P_4 s of *E. childei* ($n = 2$) from Abbey Wood and *Ectypodus* sp. cf. *E. childei* ($n = 4$) from Four Mile have eleven—a range of variation that is common for P_4 s of neoplagiaulacid species. On the other hand, a greater sample of P_4 s from these localities showing a consistently bimodal distribution in serration number may indicate that the late Wasatchian species of *Ectypodus* from the Wind River Basin is specifically distinct from the early Wasatchian *E. childei* and *Ectypodus* sp. cf. *E. childei*. In either case, the species of *Ectypodus* represented by the P_4 described here is very closely related to *E. childei*. P_4 s of the latter and *Ectypodus* sp. cf. *E. childei* have a higher lateral profile and a higher first serration than those of *E. tardus*, and a lower posterior profile than a recently recovered P_4 of the late Eocene *Ectypodus* sp.

The two molars from the Deadman Butte locality closely resemble those of a number of species of neoplagiaulacids described from Eocene and early Oligocene horizons—species of *Ectypodus* and *Pa-rectypodus* that are recognized and differentiated by the morphology

of the last premolars rather than the molars. Isolated neoplagiaulacid molars are in general very difficult to identify to generic, much less specific, level; those of certain species of *Ectypodus* and *Parectypodus* (Krause, 1982) are virtually identical. Among known Eocene neoplagiaulacids, the Deadman Butte material bears comparison to molars of *E. tardus*, *E. lovei*, *Ectypodus* sp., and *Parectypodus* n. sp. Unfortunately, molars of *Ectypodus* sp. cf. *E. childei* are not known (Krause, 1982); those of *P. simpsoni* are much larger.

The M_1 is slightly longer than that of *E. lovei* ($L = 1.4-1.6$; $W = 0.8-1.0$; Krishtalka and Black, 1975), barely shorter than that of *Parectypodus* n. sp. ($L = 1.8-2.2$; $W = 0.9-1.1$; Krause, 1982), and within the range in size of M_1 of *E. tardus* ($L = 1.6-1.9$; $W = 0.7-0.9$; Krause, 1982) and *Ectypodus* sp. ($L = 1.6-1.95$; $W = 0.9-1.2$; Krishtalka and Black, 1975). The cusp formula of 6:4 agrees with that of *E. lovei* (6:4) and *Parectypodus* n. sp. (6-8:4) and is not significantly different from those of *E. tardus* (7-8:4-5) or *Ectypodus* sp. (7-8:4). A finer measure of taxonomic affinity of M_1 may be its length/width ratio and crown outline. M_1 s of late Eocene *E. lovei* ($L/W = 1.67-1.75$, mean = 1.68, $n = 6$) and *Ectypodus* sp. ($L/W = 1.6-1.8$, mean = 1.68, $n = 8$) have a lower length/width ratio than those undoubtedly assigned to *E. tardus* (Krause, 1982; $L/W = 1.89-2.43$, mean = 2.17, $n = 4$) and *Parectypodus* n. sp. (Krause, 1982; $L/W = 1.91$, $n = 1$) as well as a more oval outline; the lateral margins of the crown are more nearly convex than straight and diverge posteriorly for much of the length of the crown. M_1 s of *E. tardus* and *Parectypodus* n. sp. have comparatively more nearly straight and parallel borders. The M_1 from Deadman Butte, with a length/width ratio of 1.94 and a somewhat oval outline, is intermediate in these features between that of late Eocene species of *Ectypodus* and early Eocene *E. tardus*, but does not differ significantly in length/width ratio from that of *Parectypodus* n. sp.

M^2 is less diagnostic than is M_1 of specific neoplagiaulacid affinities. The M^2 from Deadman Butte is larger than described M^2 s of *E. tardus* and *E. lovei*, closer in size to that of *Ectypodus* sp., and equal in length to the only known (and broken) M^2 of *Parectypodus* n. sp. (Krause, 1982). Its cusp formula of 1:3:3 is the same as that of M^2 of all of these species.

The molars from Deadman Butte are referred, tentatively, to *Ectypodus* sp. cf. *E. childei*, the neoplagiaulacid represented by a single P_4 from the Viverravus locality. Two observations make this assignment plausible: 1) the relative size of the three teeth described here is, at least, not inconsistent with that of P_4 , M_1 , and M^2 of other species of *Ectypodus*; 2) both P_4 and M_1 from the Deadman Butte area are morphologically intermediate between those of early Eocene *E. tardus* and late Eocene species of *Ectypodus*.

SUMMARY AND CONCLUSIONS

The Deadman Butte and Viverravus localities occur in a hitherto unrecognized lithostratigraphic unit of the Wind River Formation exposed in the Deadman Butte area of the Wind River Basin. This "lower gray sequence" is lithologically distinct from any named member of the Wind River Formation, as they are currently defined, and underlies sediments attributable to the Lost Cabin Member of that formation. The mammalian fauna from the Deadman Butte and Viverravus localities are Lostcabinian (late Wasatchian), as they resemble the fauna derived from localities in the Lost Cabin Member of the Wind River Formation (Guthrie, 1971) and, specifically, as is indicated by the presence of *Lambdaotherium popoagicum*.

Three neoplagiaulacid teeth—a P_4 from the Viverravus locality, and an M_1 and M^2 from the Deadman Butte locality—represent the first known record of multituberculates from the late Wasatchian. This is not an unexpected occurrence, given the presence of neoplagiaulacids in early Wasatchian as well as Bridgerian through Chadronian deposits in North America. Underwater screening of fossiliferous sediments from known and new Eocene and Oligocene localities will undoubtedly result in the recovery of more multituberculate remains and a less biased understanding of multituberculate diversity and evolution during the middle and late early Tertiary.

The premolar and, more tentatively, the molars are assigned to *Ectypodus* sp. cf. *E. childei*, a species recently described from the early Wasatchian Four Mile Fauna, Colorado (Krause, 1982), but, with recovery of additional remains, they may prove to represent a new species of *Ectypodus*. The P_4 and M_1 are distinct from and morphologically intermediate between early Wasatchian *E. tardus* and Uintan-Duschesnean species of *Ectypodus* in a number of taxonomically significant character states.

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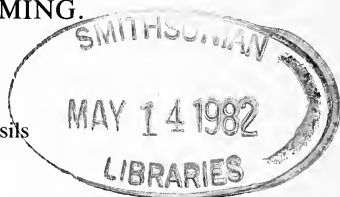
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ARTICLE 4

REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 2. GEOLOGIC SETTING

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ABSTRACT

The sediments of the Wind River Formation, Wyoming, and the fossils they contain, have been studied for over 100 years. The Wind River Formation in the area of its northeastern exposure is divided into two superimposed lithologic units, the Lysite Member below and the Lost Cabin Member above. The major lithologic differences between these members is in the color of the included claystones and mineralogy of the sandstones. The contact between these two members is not visible in surface outcrops but appears nearly conformable.

There are also two faunal units present in the area under discussion. These biostratigraphic units appear to be restricted to their respective members of the Wind River Formation, though a few faunal elements of the younger Lostcabinian are present in the upper levels of the Lysite Member.

Fossil material from the Wind River Formation is believed to have been buried on the overbank floodplain of meandering streams, and only subjected to minimal amounts of subaerial exposure before initial burial.

INTRODUCTION

Early Tertiary sediments in the Wind River Basin of Wyoming have been recognized for over a century (Meek and Hayden, 1861). Numerous studies have been concerned with the geology of this area since then. Detailed reviews of the history of investigations in this area have been provided by several authors (Keefer, 1965; Guthrie, 1967, 1971) and need not be repeated here.

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Keefer (1965) provided the most complete map of the boundaries of the entire Wind River Formation along with the most complete description of the formation in all parts of the Wind River Basin. The present study is concerned with only the northeastern part of the basin and the exposures of the Wind River Formation in this area. This area includes exposures from T39N in the north to T37N in the south and R91W to the west and R87W to the east (see Fig. 1).

The Wind River Formation was first recognized by St. John (1883). Granger (1910) was the first to recognize two distinct lithologies in this area, later named the Lysite and Lost Cabin Members (=Formations; Sinclair and Granger, 1911). Tourtelot (1946, 1953) provided the most complete description and definitions of the Lysite and Lost Cabin Members and was the only author to attempt to map the extent of these units in the northeastern part of the Wind River Basin and provide stratigraphic sections of each member. Tourtelot (1946) distinguished the two members of the Wind River Formation on the basis of the composition of the conglomerates, color of the claystones, presence of mica in the sandstones, and lateral changes in the claystones. The distinction most strongly stressed by later authors was the presence of Paleozoic rocks in conglomerates from the Lysite Member and Precambrian rocks in conglomerates from the Lost Cabin Member (Keefer, 1965; Love, 1978), although there is some variability in composition in each member (discussed below).

Granger (1910) and all later authors considered the Lysite Member as subjacent to the Lost Cabin Member. Tourtelot (1946) believed that the contact between the two members was conformable and gradational through 30 m of section. He mapped this transitional zone (Tourtelot, 1946, 1948) as a band 1.5 to 3 km wide that extended roughly east-west across the area. Tourtelot (1946) provided several stratigraphic sections of both members but did not present one of the transitional zone. Later, Tourtelot (1953) mapped the boundary between the members as a single dashed line, but maintained that there was a transitional sequence between the members. This latter boundary has been followed by virtually all later authors.

Keefer (1965) was the first to suggest that the contact between the Lysite and Lost Cabin Members was unconformable. He based this suggestion on the presence of Paleozoic rocks in conglomerates recovered from a well core drilled through rocks of Lost Cabin lithology near the Lysite-Lost Cabin contact. He also cited an area in the southeastern part of the basin where traceable Lost Cabin rocks sit unconformably on top of sediments identified as the Lysite Member, though these rocks differed in lithology from those of the type area of the Lysite Member.

Guthrie (1967, 1971) suggested that parts of the Lysite and Lost

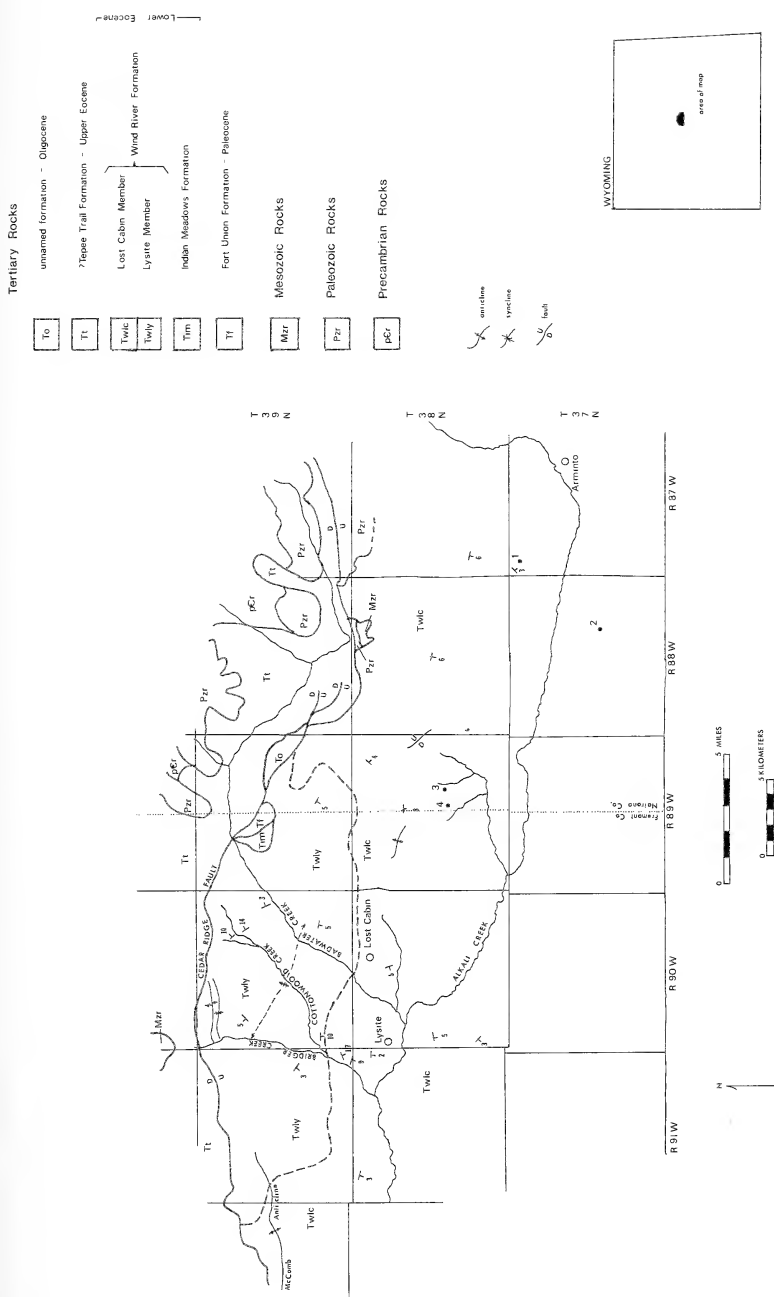


Fig. 1.—Geologic map of the northeastern Wind River Formation (modified after Tourtelot, 1953). Numbered localities indicate four main collecting localities of the Lost Cabin Member (Guthrie, 1971).

Cabin Members are contemporaneous, and accepted Tourtelot's idea of the transitional zone between the members.

LITHOLOGY

Lysite Member

The type area of the Lysite Member of the Wind River Formation is in the W $\frac{1}{2}$ T39N, R89W, along Cottonwood Creek, Fremont County, Wyoming (Sinclair and Granger, 1911; Tourtelot, 1948; Keefer, 1965). The areal extent of this member is quite limited (Fig. 1). It is bounded to the north by the Cedar Ridge Fault which trends roughly east-west. Rocks of the same lithology as the Lysite Member can be traced from the type area along the Cedar Ridge Fault both eastward and westward for about 10 km. Lysite rocks extend only 3.5 to 5 km south of the type area. Rocks of identical lithology to those of the type area of the Lysite Member were not observed anywhere else in the Wind River Basin, though some beds of slightly different lithology have been identified as the Lysite member along the southeastern boundary of the Wind River Basin (Keefer, 1965).

The Lysite Member is overlain by the Lost Cabin Member of the Wind River Formation. Nowhere in the areas surrounding the type area of the Lysite Member is there a visible contact with the Lost Cabin Member on the surface exposures. The contact of the Lysite Member with the Lost Cabin Member has been called both conformable (Tourtelot, 1946, 1953; Guthrie, 1967, 1971) and unconformable (Keefer, 1965; Love, 1978). The Lysite Member is underlain unconformably by the Indian Meadows Formation (see Tourtelot, 1953; Keefer, 1965).

Originally, the Lysite Member was believed to be the lower 100 m of the Wind River Formation (Granger, 1910; Sinclair and Granger, 1911). Tourtelot (1953) cited the thickness of the member as 90 to 180 m. Based on well log data, Keefer (1965) determined the thickness of the member to be about 1000 m.

The presence of upper Paleozoic and Mesozoic clasts in the conglomerates of the Lysite Member has been used to distinguish it from the Lost Cabin Member (Tourtelot, 1946, 1953; Keefer, 1965; Love, 1978). Conglomeratic layers are most common in the northern boundary of the Lysite Member along the Cedar Ridge Fault and diminish in size and number southward. Keefer (1965) reported 180 m of conglomerates along the Cedar Ridge Fault. Tourtelot (1946) cited boulders as large as 6.5 m in diameter also from this area.

The conglomeratic lenses are wedge-shaped or lenticular in cross-section and limited to several meters in areal extent (Fig. 2A). The size of clasts ranges from boulder sized along the northern boundary to cobble sized about 3 km south of the ridge to pebble sized another 1.5 km south. Conglomeratic lenses further south in the Lysite Mem-

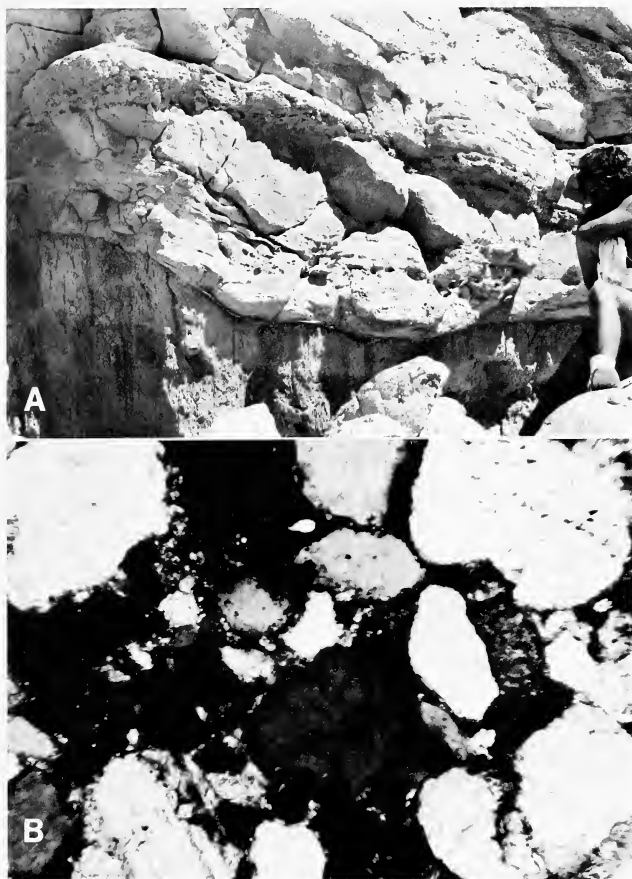


Fig. 2.—Lysite sandstones. A) Base of a large sandstone body along Lysite Rim in the type area of the Lysite Member showing the irregular base and conglomeratic lenses. B) Photomicrograph of a sandstone from the type area of the Lysite Member consisting predominantly of subrounded to subangular quartz grains and minor amounts of feldspar (lower left corner) under crossed polarized light. Scale $\times 60$.

ber do not contain clasts larger than pebble size. Nearly all of the clasts are well rounded and consist of carbonates, sandstone, quartzite, and chert. Along Noble Ridge (sec. 8, T39N, R90W) some conglomerates consist entirely of angular chert fragments. Keefer (1965) suggested that all of the rock types from the Paleozoic sequence of the Owl Creek Mountains, directly to the north, were represented in the Lysite conglomerates. Tourtelot (1946) reported Precambrian rock fragments in the conglomerates in the uppermost part of the Lysite

Table 1.—*Percentage composition of sandstones from the Wind River Formation based on point counts of prepared thin sections. Lithology 1 = sandstone from the type area of the Lysite Member; lithology 2 = sandstone from the level of the type area of the Lost Cabin Member (yellow layer); lithology 3 = same as for lithology 2 (concretionary layer); lithology 4 = sandstone from the Lost Cabin Member 320 m above the type area sandstone.*

Minerals	Lithology			
	1	2	3	4
Quartz	70	55	45	32
Calcite	27	31	43	62
Feldspar	2	1	1.5	0
Rock fragments	0	4	5	1
Biotite	0	8.5	6.5	5
Opakes	1	0.5	1	0

Member. Conglomerates occur in association with sandstone layers, at or near the base of the sandstones.

Sandstone layers are the most prominent ledge forming beds in the Lysite Member. All sandstone bodies are lenticular in shape. The thickest beds of sandstones are a maximum of 12 m thick and extend laterally for about 0.8 to 1 km. Most smaller sandstone lenses are only a few meters thick and do not extend more than a few tens of meters laterally. All are light brown to white in color, and consist almost entirely of a calcite cemented subrounded quartz sand with a minor amount of microcline feldspar and opaque minerals (Table 1, Fig. 2B).

The base of the larger sandstones is often irregular. The smaller sandstone bodies are relatively flat on top and bottom, and consist of medium to fine well sorted sand size particles throughout. In the larger sandstone bodies, one or many fining upward sequences are present. These beds are frequently cross-bedded with thin layers of pebble to granule size conglomerates near the base of the fining sequence.

Tourtelot (1946) and nearly all subsequent authors cited the presence of "white mica" in the Lysite sandstones. No muscovite or other mica was present in the thin sections examined in the present study.

The variegated claystones are the most distinct layers in the Lysite Member. These layers are predominantly brick red, light brown, and white (Granger, 1910; Sinclair and Granger, 1911; Tourtelot, 1946, 1953; Keefer, 1965; Guthrie, 1967, 1971; Love, 1978). Tourtelot (1946) noted that these brightly colored beds graded laterally into gray and drab claystones. In the type area and westward, small layers of purplish-red and green claystones are present. These colors are rare and very limited in extent (Fig. 3).

The red, brown, and white claystones vary in thickness and are



Fig. 3.—Exposed variegated claystones in the type area of the Lysite Member. Note the variable thickness and lateral extent of the color bands.

continuous only over short distances. They are arranged roughly horizontally but frequently follow the outline of overlying or underlying sandstone bodies. All of these beds are composed predominantly of illite and kaolinite, with some lesser amounts of montmorillonite (Van Houten, 1948).

Lost Cabin Member

The type area of the Lost Cabin Member is in the NE 1/4 of T38N, R89W, along Alkali Creek, Fremont County, Wyoming (Tourtelot, 1948; Keefer, 1965). The distinct variegated beds of the Lost Cabin Member can be traced eastward to the southeastern limit of the Wind River Basin, about 40 km from the type area. To the west, the Lost Cabin beds can be recognized in the Boysen Reservoir Area (White, 1952) and in the southernmost extent of the basin south of Riverton, Wyoming (Sinclair and Granger, 1911; = Big Sand Draw area), up to 90 km from the type area. Tourtelot (1953) estimated the thickness of the Lost Cabin Member as 180 to 260 m. Keefer (1965) suggested that it may be as thick as 650 m.

Tourtelot (1946) characterized the Lost Cabin conglomerates as containing rocks of Cambrian and Precambrian age. Conglomerates are most common along the Cedar Ridge to the north. Keefer (1965) cited boulders up to 2 m in diameter in this area. Southward, conglomerates become rare and occur as pebble or granule-sized clasts in coarse sandstone. Conglomeratic lenses along the Cedar Ridge contain some carbonates, sandstone, and chert, as in the Lysite conglomerates.

Slightly farther south, conglomerates contain rounded clasts of gneiss, granite, and quartzite or sandstone. Chert is also commonly present in the Lost Cabin conglomerates. In the type area of the Lost Cabin Member, conglomerates are nearly absent.

Sandstones of the Lost Cabin Member are more continuous than those from Lysite. Single units can be traced over a distance of several kilometers until the unit disappears beneath the surface. In the lowest part of the Lost Cabin Member, near the Lysite boundary (SW $\frac{1}{4}$, T39N, R91—to the west; SE $\frac{1}{4}$, T39N, R89W—to the east; N $\frac{1}{2}$, T38, R89 and 90W—to the south) sandstones are thin, varying from a few centimeters to a few meters in thickness, and dark gray in color. Higher in the section, and farther south, sandstones are thicker, up to 12 m. Granger (1910, Pl. XXII, Fig. 2) was the only author to describe and figure these thicker sandstones. The lower part of these thicker sandstones is yellow, poorly indurated, and weathers to vertical cliffs. On top is a dark gray, cross-bedded well indurated sandstone. Near the center of the bed are small to large rounded masses of the darker indurated sandstone in a matrix of the softer yellow sandstone. Granger (1910) referred to the upper gray sandstone as "concretionary" sandstones. In thin sections from these two sandstones, the percentage of calcite cement is 31% in the lower yellow sandstone, and 43% in the "concretionary" sandstones (Table 1, Fig. 4). Cross-bedding appears to be lacking in the yellow sandstone merely because it is so poorly cemented that the weathered surface does not preserve this feature.

Still higher in the section, the sandstones are dark gray, indurated, and relatively thin. These sandstones are not as common in the Lost Cabin Member as in the Lysite Member and are nearly identical to the upper "concretionary" sandstones described above.

Like the Lysite sandstones, the Lost Cabin sandstones are well sorted. The fining upward sequence of the Lysite sandstones is not so evident in the Lost Cabin. The grains are subangular to angular. The major lithological difference between the Lost Cabin and Lysite sandstones cited by Tourtelot (1946) and later workers was the presence of biotite in the Lost Cabin sandstones. In the thin sections studied, the amount of biotite varied from 5 to 8.5% of the points counted. One character of the Lost Cabin sandstones not previously noted is the presence of rock fragments. In all thin sections examined, approximately 3% of the points counted were well rounded fragments of quartzite (see Table 1, Fig. 4). The proportion of calcite cement to quartz grains is much higher than that of the Lysite sandstones. Sandstones from higher in the Lost Cabin have an even greater proportion of calcite (Table 1, Fig. 5).

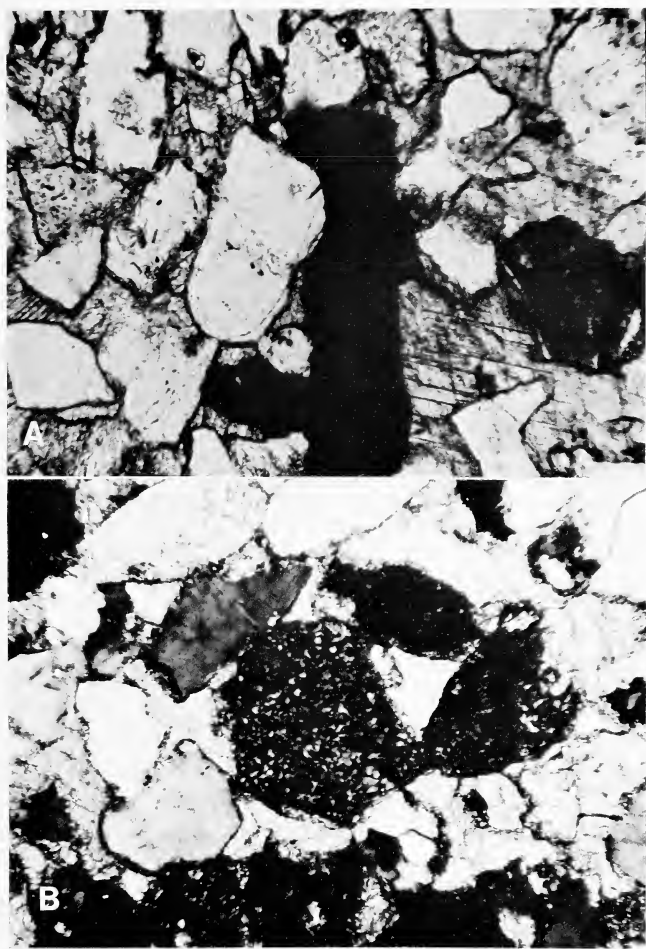


Fig. 4.—Photomicrographs of sandstones from the same level as the type area of the Lost Cabin Member (see Granger, 1910: Pl. XXII, Fig. 2). A) Photomicrograph in plane polarized light showing subrounded to subangular quartz grains, biotite grains (dark mineral), and calcite cement. Scale $\times 60$. B) Photomicrograph in crossed polarized light showing quartzite fragment (center).

Again, as in the Lysite Member, the most easily distinguished feature of the Lost Cabin beds is the color of the claystones. Virtually all authors, beginning with Granger (1910) have noted the marked difference in the coloration of claystones from the two members. The Lost

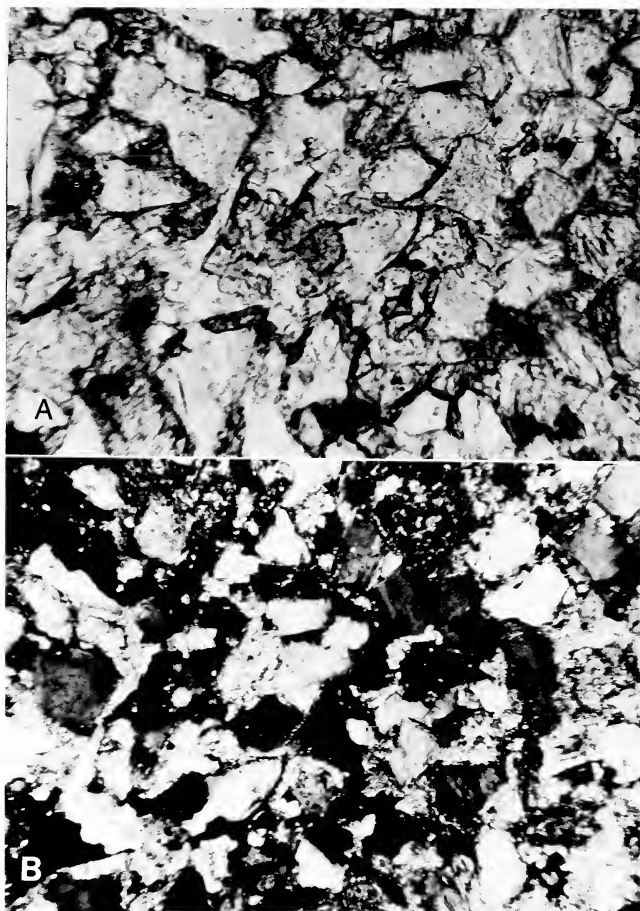


Fig. 5.—Photomicrographs of sandstones from 300 m above the type area sandstones in the Lost Cabin Member in plane polarized light (A), and crossed polarized light (B) showing angular to subangular quartz grains and high amount of calcite cement. Scale $\times 60$.

Cabin claystones are reddish-purple and light gray in color. Tourtelot (1946) noted that laterally these beds grade into more sandy claystones that are green in color. These green sandy claystones occur north of the type area in the NW $\frac{1}{4}$ of T38N, R88W and NE $\frac{1}{4}$ of T38N, R89W. Also in this area are thin beds of claystone that are dark blue. These are relatively rare and not very continuous laterally.

DEPOSITIONAL ENVIRONMENT

Keefer (1965:A53) suggested that the conglomerates of the Wind River Formation were deposited as alluvial fans along the flanks of the Owl Creek and Big Horn Mountains to the north, and the remaining sediment in the interior part of the basin was part of channel deposits and outwash plains. Kraus (1980) interpreted sandstones from the early Eocene of the Big Horn Basin similar to those in the Wind River Formation as being formed by a slow moving, meandering river.

The modern environment which appears closest to the depositional environment of the Wind River Formation is that of a tropical or "wet" alluvial fan system. Several authors (Gole and Chitale, 1966; Schumm, 1977; Reineck and Singh, 1980) have described modern tropical alluvial fans. These alluvial fan systems have many of the characteristics of the sediment of the Wind River Formation.

The head fan area of "wet" alluvial fans contains the coarsest size particles but extends only a short distance distally (about 16 km in the alluvial fan of the Kosi River, India, Schumm, 1977). This is also true of the Wind River sediments. The coarse conglomerates of both members are common only along their northern boundary and are almost totally absent 8 km to the south.

The mid-fan area is characterized by numerous stream channels with the conglomerates containing particles of granule to pebble size (Reineck and Singh, 1980). The sandstones of the Lysite Member fit this description. There are many channel sandstones that are limited in extent and variable in thickness, implying a system of channels that may have remained stationary for relatively short periods of time.

The distal fan in a humid environment is made of laterally shifting streams. The Kosi River in India has continually moved its channel eastward for the last 200 years over a distance of approximately 100 km (Schumm, 1977). The slow progression of this channel would leave a relatively thick continuous bed of sand across the distal fan area and beyond. This is precisely the type of sandstone body common in the type area of the Lost Cabin Member. This model of a distal fan river would also apply to the sandstone bodies in the Big Horn Basin suggested as meandering river deposits (Kraus, 1980).

The model of a tropical alluvial fan sequence is also consistent with the environment of the early Eocene in the Wind River Basin that was interpreted on the basis of fossil plants as wet subtropical (MacGinitie, 1974).

The claystones of the Wind River Formation have been long considered overbank floodplain deposits (see Van Houten, 1948). Virtually all authors have followed this interpretation. The reasons for color-

ation of the claystones, however, has long been in dispute. Explanations for the color banding in the claystones have been: 1) deposition of sediment from different colored source rocks; 2) redeposition of previously formed red soils; 3) diagenetic iron-mineral formation; or 4) soil formation (see Van Houten, 1948).

Bown (1979) and Bown and Kraus (1981a) have interpreted all of the color banding in the claystones of the early Eocene Willwood Formation in the Big Horn Basin as representing paleosol horizons, and suggested that similar horizons were present in the Wind River Basin (Bown and Kraus, 1981b). No detailed chemical or microstratigraphic analysis of the claystones in the Wind River Formation was done in the present study. However, according to field examinations of the variegated claystones, none of the features of the Willwood "paleosols" (Bown and Kraus, 1981a:6-7) are readily observable in the Wind River claystones, nor is any recognizable repeated sequence of colors noticeable. In discussing the possible causes of the color banding in the claystones of the early Eocene basin deposits of Wyoming, Van Houten (1948:2110) stated, "Any soil that does form probably would be 'alluvial soil', showing little or no modification excepting a slight accumulation of organic matter in the surface (Kellog, 1941:340). As a result of continual aggradation there is little chance for development of a soil profile, hence the characters of the alluvial soil 'are determined largely by the nature of the materials from which they have been derived and the manner in which these materials have been sorted and deposited' (Albeiter and others, 1938:1133)."

Results from the paleomagnetic studies show that there is a great deal of altered iron minerals especially in the red claystones. This would support the theory of diagenetic production of the color bands.

STRUCTURE

The major structure present in the Lower Eocene sedimentary rocks in the northeastern part of the Wind River Basin is the Cedar Ridge Fault, which runs roughly east-west and is the northern limit of the Wind River Formation in this area (see Tourtelot, 1953). It is a normal fault that is late early Eocene in age (Love, 1978).

The strata of the Wind River Formation dip gently southward toward the center of the basin at an angle of 3° to 6°. The only major fold present in the area is the McComb anticline which parallels the Cedar Ridge Fault across sections 16, 17 and 18 of T39N, R91W and farther westward (Tourtelot, 1953). A few additional folds are present in the area along the Cedar Ridge Fault but are limited in extent. Tourtelot (1953) also mapped two small anticlines farther south of Cedar Ridge. Both trend roughly northwest-southeast. The first is about 3 km south



Fig. 6.—Anticline exposed along Lysite Rim in the type area of the Lysite Member. Beds in the northeast (upper left) dip to the northeast, and in the southernmost extent of the rim (lower right) dip to the southwest. Exposure approximately 10 km long.

of the Cedar Ridge Fault (sec. 13, T39N, R90W and sec. 18, T39N, R89W). The other is north of the type area of the Lost Cabin Member (sec. 16, T38N, R89W). Keefer (1970) mapped a few anticlines in the subsurface in this area, but these features are not present in the Eocene strata.

A broad anticline, which has not been previously mapped, is in the type area of the Lysite Member. The entire cross-section of this fold is exposed in a steep escarpment along the eastern bank of Cottonwood Creek, termed Lysite Rim (Fig. 6). The first small anticline mentioned in the previous paragraph (3 km south of Cedar Ridge plotted by Tourtelot, 1953) appears to be only the northern limb of an anticline. The beds dip an average of 15° to the northeast along this limb. Southwest of this area along Lysite Rim, dips range from 2° to 3° and appear fairly random. At the southwestern end of Lysite Rim (sec. 36, T39N, R91W) the rocks dip to the south and southwest from 10° to 20° .

Tourtelot (1953) mapped a few minor faults in the Wind River Formation along the Cedar Ridge Fault. He also mapped a probable fault at the southern end of Lysite Rim that ran east-west through the center of sections 35 and 36, T39N, R91W. This fault also marked the contact

between the Lysite and Lost Cabin Members. Later, Keefer (1970) mapped this same fault as definitely present. However, there is no evidence for a fault in the surface exposures examined in the present study. The area where this fault is supposed to be present is the southern limb of the previously described anticline. All of the sandstones exposed in this area appear continuous. The claystones in this area are covered with vegetation or Quaternary alluvium and cannot be identified. The sandstones are of Lost Cabin lithology.

GEOLOGIC HISTORY

Keefer (1965, 1970) presented the most complete depositional and structural history of the entire Wind River Basin. Love (1978), summarizing the history of the Wind River Basin in its northeastern part, recognized seven depositional events and six tectonic events from the Paleocene through the Miocene. He viewed the deposition of the Lysite and Lost Cabin Members (depositional events 3 and 4) as the result of separate events of renewed uplift of the Big Horn Mountains and Casper arch to the north and east (tectonic events 3 and 4), and suggested that some 300 m of the Lysite Member was eroded before the deposition of the Lost Cabin Member.

As mentioned previously, no contact between the two members of the Wind River Formation is visible in surface outcrops in the northeastern part of the basin. Keefer (1965), who first proposed that the contact between the two members was unconformable, based his conclusion on two factors: the presence of carbonate rocks in conglomerates taken from a well core in the area; the relationship of rocks exposed in the southeastern margin of the basin. These were interpreted as representing the two members though they differed slightly in lithology from those at the type area. In his proposal he stated, however, the lack of reliability of using the composition of conglomerates as distinct boundaries.

If there is indeed an unconformable contact between the two members, it is undetectable in the northeastern part of the basin. Any angular unconformity would have to be no more than a few degrees because no marked change in the dip of surface exposures can be seen.

FAUNAL CORRELATION

As early as 1910, Granger recognized two distinct faunal levels of the Eocene in the northeastern part of the Wind River Formation. The presence of two genera of titanotheres, *Lambdaotherium* and *Eotitanops*, was used as an indicator of the upper (Lost Cabin or *Lambdaotherium*) zone, and their absence as indicative of the lower (Cottonwood Creek or Lysite) zone (Granger, 1910; Sinclair and Granger, 1911).

These faunal levels were associated with the two lithologic units present in the area, the Lysite and Lost Cabin Members of the Wind River Formation. Later, Granger (1914) identified additional faunal levels from early Eocene rocks in the Bighorn Basin that were older than the Lysite and Lost Cabin faunal levels. Van Houten (1945) made a detailed comparison of the faunal levels defined by Granger for the early Eocene and recognized three levels—Gray Bull, Lysite, and Lost Cabin. He suggested that the Lysitean was the most poorly defined and might just represent the latest Graybullian level. However, all three substage names have been used by every author who has discussed early Eocene faunas from North America since Van Houten's discussion.

Most descriptions of the mammalian fauna from the Lysite and Lost Cabin beds have come as a part of monographs dealing with the systematics of a single group, such as condylarths (Loomis, 1905; Gazin, 1968; West, 1976), primates (Loomis, 1906; Szalay, 1969, 1976), artiodactyls (Sinclair, 1914), perissodactyls (Osborn, 1929; Kitts, 1956; Radinsky, 1963), rodents (Loomis, 1907; Wood, 1962, 1965), or insectivores (West, 1973; Krishtalka, 1976). In a series of papers, Matthew and Granger (Matthew, 1915*a*, 1915*b*, 1915*c*, 1918; Granger, 1915) included the entire fauna from both the Lysite and Lost Cabin beds in their overall review of early Eocene mammals from North America.

The entire Lysite fauna has been studied by Kelley and Wood (1954) and Guthrie (1967). The entire Lost Cabin fauna has been studied only by Guthrie (1971). Currently a major review, of both the Lysite and Lost Cabin faunas is being undertaken by several workers at the Carnegie Museum of Natural History.

The most recently published faunal lists of the Lysite and Lost Cabin faunas were presented by Guthrie (1967, 1971). He cited several differences in the two faunas on the generic and specific levels but maintained that the occurrence of *Lambdaotherium* was the major faunal difference. However, he did report a single tooth of *Lambdaotherium* from beds of Lysite lithology that he believed represented the upper most part of the Lysite Member. This specimen was recovered in the Dolis Hill area (sec. 26, T39N, R91W), southwest of the type area of the Lysite Member (D. Guthrie, personal communication, June, 1981). Because of the presence of *Lambdaotherium* in the Lysite Member he suggested that the biostratigraphic boundaries were not coincident with the lithological boundaries of the two member, contrary to the view of all previous authors.

The presence of *Lambdaotherium* in the Lysite Member does not automatically include its faunas in the Lostcabinian biostratigraphic substage. Its occurrence could simply mean a range extension for

Lambdotherium. However, additional specimens possibly referable to Lostcabinian species recently collected from the upper levels of the Lysite Member may support Guthrie's suggestions.

The lowest level of the Lysite Member where fossils have been recovered is in the low relief area on the western side of Cottonwood Creek in the type area. Rocks of the Lysite Member extend stratigraphically approximately 300 m above this point. The highest level in the type area is 80 to 100 m above the lowest fossiliferous level. All of Guthrie's (1967) collections of fossils from the Lysite Member were within this 80 to 100 m zone. The *Lambdotherium* specimen from Dolis Hill, although the exact level was not recorded, was stratigraphically at least 30 m above the highest point in the type area. The additional material possibly referable to Lostcabinian species has been recovered from rocks of the Lysite Member east of Badwater Creek, which are also stratigraphically 30 to 40 m above the highest levels in the type area.

Two fossil localities along the east bank of Badwater Creek that have produced a small fauna which contains Lostcabinian species are the White Trash Quarry (NE $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 17, T39N, R89W) and the Fross Quarry (NW $\frac{1}{4}$ sec. 19, T39N, R89W). Together these two localities have produced two partial M_3 s of *Lambdotherium* and an isolated lower molar of *Microsyops scottianus*. Both these taxa have previously been described only from the Lost Cabin fauna. Two species recovered from these localities are exclusively Lysitean, *Absarokius abbotti* and *Microsyops latidens*. The remainder of the fauna consists of the following animals known from both levels: *Phenacodus* sp., *Macrocranium nitens*, *Bunophorus etsagicus*, *Hyracotherium* cf. *H. index*, *Notharctus* or *Pelycodus* sp., ?*Viveravus* sp., *Paramys copei*, *Knightsomys depressus*, and *Heptodon* sp.

Another quarry farther east of Badwater Creek (center sec. 27, T39N, R89W) is approximately 125 m above the White Trash and Fross Quarries stratigraphically. This fauna is still well within the Lysite Member, but is the highest level from which fossils have been recovered in that member. It is at a level about 40 m below the contact with the Lost Cabin Member. Unfortunately the fauna from this locality is known from only a few specimens. The species present are *Hyopsodus* sp. (large), *Phenacodus* sp., *Hyracotherium* sp., carnivore indeterminate, *Coryphodon* sp., and an indeterminate rodent. None of these species are characteristic of only one or the other faunal level.

Still farther east, in rocks of Lost Cabin lithology (adjacent corners of sections 1, 2, 11, T38N, R89W), a small fauna containing *Lambdotherium* has been recovered. This locality (labeled either "Turtle Blues" or "Oakie Trail" Quarry on specimens in the Carnegie Museum systematic collections) represents the lowest level at which fos-

sils have been collected in the Lost Cabin Member. It is about 40 m above the presumed Lysite-Lost Cabin boundary. The only other species from this locality are *Hyracotherium* sp., *Coryphodon* sp., *Hyopsodus* sp. and ?*Uintacyon* sp. Again, none of these species are limited to either faunal level.

The three additional specimens of mammals characteristic of the Lostcabinian biostratigraphic substage that appear in the upper 200 m of the Lysite Member appear to support Guthrie's (1967, 1971) statement that the Lostcabinian substage is not coincident with the lithologic boundaries of the Lost Cabin Member. However, the evidence present here is by no means conclusive. To verify Guthrie's statement, more extensive collections of fossil material are needed from the upper part of the Lysite Member.

Guthrie (1971) cited four main localities from which nearly all of the fossil material from the Lost Cabin Member was collected (numbered 1, 2, 3, and 4; see Fig. 1). He stated that all four localities were stratigraphically within 12 m of one another. However, it is evident from the altitude of the localities and the southward dip of the beds that this cannot be true. According to the determined attitude of the Lost Cabin strata, the lowest of Guthrie's (1971) localities are 3 and 4, which are at about the same level. Locality 1 is stratigraphically 90 to 100 m above 3 and 4. Locality 2 is considerably higher in the section than locality 1, somewhere between 125 and 250 m above it.

TAPHONOMY

Nearly all fossil remains from both members of the Wind River Formation come from the claystones. Rarely, skeletal elements of turtles and crocodiles can be found in the sandstone layers of both members. Some small lenses of conglomerate in the type area of the Lysite Member have granule-sized bone chips included in them. Other than these few exceptions, the remainder of the known fossil material comes from the variegated claystones.

Guthrie (1967) believed that the majority of the mammalian fossils from the Lysite Member came from the brick red claystones, and the light colored claystones yielded predominantly remains of turtles and crocodilians. He later (Guthrie, 1971) suggested that nearly all of the fossils collected at three of the main localities of the Lost Cabin Member (his localities 1, 2, and 3) were from a single maroon claystone layer, and that at the fourth locality, the fossils were from an equivalent layer of dark gray shale. However, as stated above, these localities are much more widely separated stratigraphically.

Fossils are consistently present in all colors of claystones in both members of the Wind River Formation. In many cases the fossils were collected on the surface and it is not clear from which color claystone

they came. Fossils do occur in "pockets" where they seem to be concentrated. The fact that these concentrations of fossils are in red claystones at Guthrie's four localities in the Lost Cabin Member is probably coincidental, although no concentrations as prolific as Guthrie's locality 1 have been found anywhere else in the area.

Bown (1979) and Bown and Kraus (1981*b*) found concentrations of fossils in the drab gray layers of the variegated claystones of the early Eocene Willwood Formation. They interpreted these layers as paleosol horizons. They contended that the accumulations were not fluvial accumulations on the basis of lack of size sorting, lack of abrasion on the bone, and evidence of subaerial exposure on some specimens. They believed that these concentrations were due to attritional accumulation over long periods of time in the upper layer of soil.

The model proposed by Bown and Kraus (1981*b*) of bone being concentrated on low spots of a floodplain during flood stage is probably correct and is consistent with the sedimentological explanation of the origin of the claystones in both the Wind River and Willwood Formations. However, the suggestion that these are attritional assemblages concentrated in soils is highly unlikely.

The climate in Wyoming during the time of deposition of the Willwood and Wind River Formations was wet subtropical (MacGinite, 1974). The only published studies of the durability of small mammal bones in a similar climate was by Payne (1965), who experimented with the decomposition of baby pigs (*Sus scrofa*) in the Carolinas. He found that after a little over a week all the flesh had been removed from the carcasses and carrion feeding insects had begun to destroy the bone. Clark and Guensburg (1970) observed that after only six weeks the bones of small mammals were totally destroyed. Korth (1979) reported that shrew (*Sorex*) carcasses were cleaned of their flesh in only three days and insects had begun to destroy the bone after only 8 days in the semiarid climate of Nebraska.

Clearly, small mammal bone could not exist on the ground surface for any prolonged period of time. Several authors have suggested various other means of their destruction and arrived at similar conclusions (Clark et al., 1967; Voorhies, 1969; Behrensmeyer, 1978).

Also, the survival of bone in the upper levels of a humid climate soil is also unlikely. Reineck and Singh (1980: 297) noted that soils formed in humid climates are acidic and heavily leached. This acidity would have destroyed the small bones of vertebrates relatively quickly.

The lack of sorting of the fossil accumulations mentioned by Bown and Kraus (1981*b*) is not consistent with their tabulations of the percentage of preservation of skeletal elements. The results given in their

tabulations (Bown and Kraus, 1981b: Tables II, III, IV) are nearly identical to those of alluvially sorted assemblages studied by Korth (1979: Table 1, Fig. 14). Korth (1979) suggested that small bone could be easily moved by very low currents of water competent to carry only the clay-sized fraction. Therefore, these bones would be sorted without being abraded. This would result in the final deposition of bones in a clay matrix.

The facts do not support the hypothesis presented by Bown and Kraus (1981b), and thus it cannot be verified at present. This does not appear to be a likely model for small mammal bone preservation in the early Eocene of Wyoming.

The bones of large mammals from the Wind River Formation are almost always unaltered but badly broken. The breaks in the bone appear to be those that occurred after fossilization (see Webb, 1969). The characteristic crushing of the skulls of the large mammals, such as *Coryphodon* and *Bathyopsis*, is due to diagenetic processes (for example compaction of clays due to dehydration). A few specimens of bones and teeth of large mammals show effects of subaerial exposure (see Behrensmeyer, 1978) but these are rare.

Small mammal bones recovered from the Wind River Formation also show a great deal of crushing and breakage acquired during diagenesis and post-fossilization exposure on the ground surface. Only one specimen recovered from the Lost Cabin Member can be interpreted as a regurgitated owl pellet. This specimen consists of a skull of *Knightomys depressus* that is separated along the cranial sutures, both associated mandibles, and some postcranial bones. No other specimens occur in coprolites or pellets. The bones were frequently concentrated in shallow depressions on the floodplain and rapidly covered with clay-to silt-sized particles by subsequent episodes of floodplain deposition. The burial of all of the bones, except for a few isolated cases of large bones, was relatively rapid. The lack of evidence for stream abrasion on the bones is not unpredicted because of the very low velocities required to transport bones of smaller mammals (Dodson, 1973), which make up the majority of the fauna recovered.

CONCLUSIONS

The Wind River Formation, in the northeastern part of the Wind River Basin, consists of two lithologically distinct members, the Lysite and Lost Cabin Members. Both are sedimentary sequences of claystone, sandstone, and some conglomerate deposited as alluvial fans and meandering stream sequences. The source of the sediment was clastic debris shed from the Owl Creek and Bighorn Mountains to the north during the early Eocene as the result of renewed uplift of these

mountains at that time. The two members were truncated along their northern boundary by the normal Cedar Ridge Fault and slightly deformed at the close of the early Eocene.

The Lost Cabin Member overlies the Lysite Member. It is uncertain whether the contact between these two members is conformable or not. According to the evidence of the surface exposures, there is no difference in the attitude of the two members around their contacts with each other.

The vertebrate fossils deposited in the Wind River Formation were concentrated on the floodplains of meandering streams and altered only slightly by taphonomic processes.

Two distinct faunal levels of the early Eocene are represented in the faunas from the northeastern portion of the Wind River Formation. It is possible that these distinct faunas do not coincide with the member boundaries of the Wind River Formation as previously believed, but the evidence is still quite scanty.

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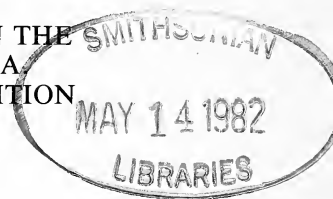
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ARTICLE 5

ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA I. CLIMATE AND FAUNAL COMPOSITION

KARL E. STREILEIN¹



ABSTRACT

Environmental unpredictability has been the predominant characteristic of the Caatinga region of northeastern Brazil in both evolutionary and ecological time. The geographic center of the Caatinga harbors a relatively depauperate small mammal fauna, including nine species of rodents in four families and three species of marsupials in a single family. Basic ecological and behavioral information are presented for each species of this little-known fauna.

INTRODUCTION

The Caatinga region of northeastern Brazil is a unique tropical biome. Whereas most of the tropics is characteristically mesic and seasonally predictable, the Caatinga is semiarid and has an unpredictable rainfall regime. In essence, the Caatinga is a large xeric island of thorn scrub vegetation surrounded by predictable, relatively mesic biomes.

The uniqueness of the Caatinga with respect to the other major tropical biomes poses many interesting questions. Which species from the surrounding mesic-adapted tropical faunas have invaded this xeric zone? How have these species adapted to the unpredictable environment? Do differences exist in the relative degree of adaptation? How are the species distributed among the various habitats and what factors

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are or were most influential in the development and maintenance of the distribution patterns?

Terrestrial small mammals are generally sedentary species, incapable either of the mobility of large mammals which can readily migrate from inhospitable areas or of bats and birds which can cover long distances in normal daily activities. These species must therefore adapt to prevailing localized conditions or fail to persist. Thus small mammals in the Caatinga should clearly exhibit adaptations to the constraints imposed by the unpredictable xeric environment.

A comprehensive analysis of a small mammal fauna must consider a wide variety of both proximate and ultimate factors which can influence species composition and patterns of distribution. The present report is primarily concerned with describing the environmental factors to which the fauna has had to adapt and with presenting baseline ecological information on each species. Subsequent reports will deal with (1) physiological adaptations (Streilein, 1982a), (2) reproduction and population ecology (Streilein, 1982b), (3) distribution patterns (Streilein, 1982c), and (4) agonistic behavior (Streilein, 1982d).

STUDY AREA

General Description of the Caatinga Physiography

Three distinct features typify the geological composition of the Caatinga (Ab'Saber, 1970). The dominant feature, in terms of area encompassed, is the basement level of Precambrian crystalline rock. In the extensive areas where this layer is exposed, surface relief is insignificant and flats or gradual slopes predominate. Numerous abrupt protrusions of granitic rock are widely distributed throughout the Caatinga in the form of low mountain ranges (serras), small mountain ridges (serrotes), and lowland outcroppings (lajeiros). These sharply delineated formations have been uncovered and shaped through the processes of erosion and denudation, frequently resulting in extremely rugged terrain. Finally, there are areas where the surface layer of sedimentary rock (primarily sandstone) has remained intact. Some of these areas are elevated above the surrounding countryside as steep-sided plateaus (chapadas).

The distinctive physiography of the Caatinga is largely attributed to the abundant, ubiquitous granitic formations. Overall spatial heterogeneity in the Caatinga is greatly enhanced by the distribution of serrotes, serras, and lajeiros of various sizes and shapes. Within these formations, the total degree of three-dimensional structural complexity is normally quite high. The sandstone and crystalline rock areas are, by comparison, relatively uniform and structurally very simple. Structural diversity in the Caatinga on both the geographic and local scales

is thus determined primarily by the number, types, and distributional patterns of the granitic formations.

Loss of the surface layer of porous sedimentary rock and the subsequent exposure of the underlying crystalline layer over much of the Caatinga has had a profound impact on the hydrological balance of the region. The compact structure of the crystalline rock and the great depth to which it extends prevent the formation of ground water. In addition, the soil layer is often sparse or totally lacking. Most of the water entering the system is thus lost via rapid runoff. The water retaining function of the sedimentary rock is dramatically demonstrated by the presence of the "oasis" of Cariri (centered at the base of the northern side of the Chapada do Araripe, approximately 60 km from the study site, near the southern edge of the Chapada) in an otherwise semiarid area. This mesic locale is situated in such a manner that it receives an abundant supply of water in the form of seepage from the sandstone of the Chapada (Markham, 1972). In general, the capacity for absorption and retention of water is negligible in the Caatinga. The geological composition of the Caatinga thus has a significant adverse effect on the hydrological balance and is instrumental in maintaining the semiarid nature of the region. If the rainfall was spread over a longer interval of time rather than the brief period typical of the Caatinga, this effect would be less pronounced.

Climate

The current geographic boundaries (Fig. 1) of the Caatinga extend from 3° to 16° south latitude and from 35° to 45° west longitude, encompassing an area of 650,000 km² (Reis, 1976; Frota-Pessoa et al., 1971). Evidence has begun to accumulate, however, which demonstrates that both the geographic limits and the degree of aridity experienced fluctuated substantially during the Quaternary.

Until recently, the climate of tropical South America was generally considered to have been relatively stable through time. This idea induced investigators to formulate the "evolutionary time" hypothesis of species diversity, which postulated that the great number of species of tropical organisms was the result of a long period of adaptation to a stable environment (Pianka, 1966). The concept of tropical zone stability was challenged by Haffer (1969) and Vanzolini and Williams (1970), who independently proposed the existence of faunistic refugia during periods of climatic change. Vuilleumier (1971) has since concluded, after reviewing the available zoological and geological data for the entire continent, that "a series of humid-arid cycles drastically and repeatedly altered vegetation patterns during the Quaternary" in tropical South America (see also Meggars, 1975, 1977; Brown, 1977a, 1977b; Simpson and Haffer, 1978). Vanzolini (1970) has also compiled

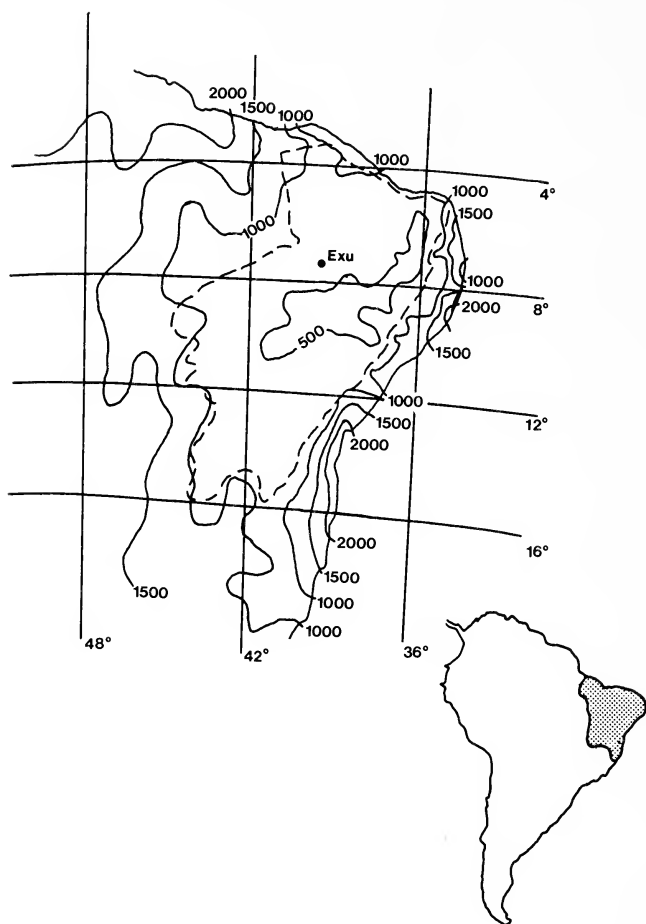


Fig. 1.—Annual rainfall in northeastern Brazil (in mm). The limits of the Caatinga are indicated by the dashed line, and approximately follow the 1000 mm isohet. Exu is the location of the study site. Modified from Reis (1976).

diverse botanical, zoological, and geological evidence which indicates that substantial climatic fluctuations altered the Amazon Basin and by extension, the neighboring Cerrado and Caatinga zones.

Contraction and subsequent expansion of the rain forest permitted the concomitant expansion and later contraction of the open formations. Various geomorphological formations, including stone lines and alluvial and lateritic deposits formed in arid climates, have been found far beyond the contemporary boundaries of the xeric zone; at one

time, an arid climate prevailed at least to Brasilia in the West and Belem and Sertanea in northwest Brazil (Vanzolini, 1970). Indirect evidence gleaned from biogeographic studies of plants and animals demonstrates a close correspondence in species composition between the now widely disjunct open formation enclaves within the Amazon Basin and the Cerrado and Caatinga. There is also faunistic evidence that the extent of the xeric zone was considerably reduced. Localized areas of orographic rainfall (brejos) within the Caatinga support humid forest habitat, and have many endemic forms peculiar to the region and radically different from those in the surrounding Caatinga, but also share numerous elements with the Amazon Forest (Vanzolini, 1970).

The occurrence of a series of wet and dry cycles in the Quaternary is now widely accepted, but the exact number of cycles and their approximate time periods have not been established. Vanzolini (1973) proposed that at least three cycles took place during the last 100,000 years, with the two latest episodes occurring approximately 11,000 (Damuth and Fairbridge, 1970) and 2600 (Vanzolini and Ab'Saber, 1968) years ago.

The Caatinga is also noted for radical short-term climatic fluctuations with regard to predictability and amount of precipitation. The extreme variability in rainfall patterns, frequently culminating in extended droughts or severe flooding, has led various authors to graphically describe this area as a "zone of calamity" (Freise, 1938), "the polygon of drought" (Eidt, 1968), and the "region of anomalous drought" (Markham, 1972). Relative to other areas of Brazil, the Caatinga also possesses some of the most extreme meteorological values recorded, including the highest insolation, lowest degree of cloudiness, highest mean temperatures, lowest relative humidity, and the most instances of scarce and irregular rainfall (Reis, 1976).

The rainfall pattern in northeastern Brazil is primarily influenced by the Southeast Trade Winds in conjunction with three large, mobile masses of air—the equatorial continental mass; the Intertropical Convergence Zone; and the South Atlantic Anticyclone (synonymous with the Atlantic Polar Front). While under the influence of the Southeast Trade Winds, the Caatinga receives no precipitation (Reis, 1976). This condition prevails during part of every year but often persists for a much longer period of time, producing the droughts characteristic of the region. No single causal mechanism has yet been discovered that can explain this phenomenon, which occurs at random intervals. Generally, the three moisture-laden air masses introduce some rain into the Caatinga in any "normal" year. The amount of rain attributable to each mass of air, however, often varies greatly from year to year. All three air masses are affected to a greater or lesser extent by the orographic features they encounter. Rainfall in any given area is also

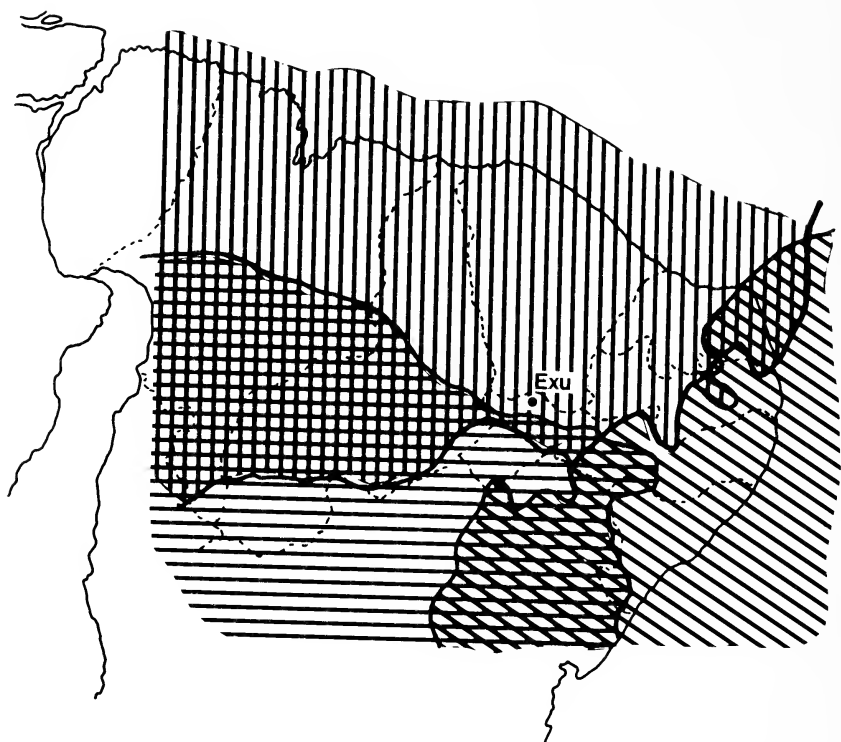


Fig. 2.—Normal extent of influence of the three major air masses affecting precipitation in northeastern Brazil. Vertical lines represent the Intertropical Convergence Zone (precipitation occurs mainly in January–April), horizontal lines represent the continental equatorial air mass (precipitation occurs mainly in November–January), diagonal lines represent the South Atlantic Anticyclone (precipitation occurs mainly in May–July). Modified from Reis (1976).

an inverse function of distance from each air mass, the exact positions of which may vary considerably between years. The normal spheres of influence for each air mass are shown in Fig. 2. Zones of overlap do not usually have significantly augmented rainfall because they occur where the influence of each air mass is reaching its limit of effectiveness. A more detailed account of the rainfall regimes and the patterns of atmospheric circulation can be found in Reis (1976) and Markham (1972).

The effectiveness of the orographic features is related to altitude, distance from the coast, and orientation with respect to the direction of advance of the three air masses. Locales which receive augmented rainfall, *brejos*, are capable of sustaining humid forest. Andrade and

Lins (1964) list 22 principal brejos in the state of Pernambuco alone, thus the number of mesic refugia is substantial. The orographic features responsible for the increased humidity of brejos also create rain shadows on the leeward side.

The climate of the Caatinga is thus distinguished by its unpredictability with respect to both evolutionary and ecological time.

Vegetation

The key characteristics of the xerophytic Caatinga vegetation are adaptations to the constraints imposed by the irregular and limited rainfall. Deciduousness during dry periods is the most common, conspicuous strategy of water conservation, while the succulents utilize the alternate strategy of long term water storage. The pronounced xerophytic adaptations of Caatinga plants, such as the many species of Cactaceae and Euphorbiaceae, strongly indicate that aridity has persisted for thousands of years in this region (Alvim, 1949).

Vegetation associations in the Caatinga range from relatively simple to extremely complex assemblages with regard to species abundance and composition, characteristic species, and foliage height profiles. In general, the boundaries of Caatinga vegetation closely parallel the 1000 mm rainfall isohet throughout northeastern Brazil (Fig. 1). A number of different types of vegetation are frequently found in a relatively small area, creating a vegetational mosaic. The terms Low Caatinga (=Caatinga Baixa) and High Caatinga (=Caatinga Alta), will be employed throughout this study as general classes of vegetation based upon foliage height profiles. Low Caatinga includes the various types of scrubby vegetation which have canopy elements generally attaining only 3 to 5 m, while High Caatinga refers to vegetation types where the dominant canopy elements are typically greater than 5 m.

Classification of vegetation with regard to foliage height arbitrarily groups a number of distinct vegetation types. Plant species characteristic of a certain type of Caatinga vegetation may include representatives of the cacti, euphorbs and/or legumes, depending upon the geographic location. The dominant species may also differ greatly between locales, while conforming to the Low Caatinga type. Within a given locale variation is also the result of microclimatic and edaphic factors, minor differences in topography, and the actions of domestic animals. The most frequently encountered form of vegetation is Caatinga Baixa; the preponderance of this form is due in part to the activities of man and various animals, especially goats.

Another general type of vegetation found within the Caatinga region is strictly associated with areas of orographic rainfall. These areas, "brejos," do not experience the intense hydrological deficits characteristic of the surrounding countryside and are thus able to sustain

humid forests which in turn differ radically from the true xerophytic Caatinga vegetation. The botanical affinities of the brejos lie with the Atlantic Rainforest (Andrade and Lins, 1964).

Study Site

Most of the field work was conducted in the municipality of Exu in the northwestern corner of the state of Pernambuco, Brazil. This is a complex area with respect to geology and vegetation. All of the three major geological features that typify the Caatinga region are found in close proximity there. The dominant element in this portion of the Caatinga is the Chapada do Araripe, an extensive sandstone plateau which stretches for hundreds of kilometers from east to west along the border of Pernambuco and Ceará. Numerous granitic outcroppings, in the form of lajeiros and serrotes, greatly enhance the structural diversity of the area in both the horizontal and vertical dimensions. The composition of the vegetation typically reflects the complexity of the area. Abrupt, drastic changes in plant species composition frequently occur over relatively small horizontal or vertical distances but gradual transitions are also common. The overall pattern may best be described as a mosaic of patches of variable size, some of which are clearly distinct while others are blurred around the edges. A few elements atypical of Caatinga vegetation are present in the flora, having invaded the area from the Chapada do Araripe. This chapada receives a substantial amount of orographic rainfall (Markham, 1972) which, in conjunction with soil conditions, permits the existence of Cerrado vegetation in the heart of the Caatinga.

The primary site studied within the municipality was at Fazenda Batente, located 6 km southeast of the town of Exu (7°31'S, 39°43'W) and approximately 10 km south of the base of the Chapada do Araripe. The fazenda contained a variety of habitat types—several lajeiros, extensive stands of low thorn scrub, pastures, agricultural fields, and abandoned fields in various stages of succession.

MATERIALS AND METHODS

Faunal Composition and Species Accounts

A permanent 12 × 12 live trapping grid (Fig. 3) was established at Fazenda Batente in January 1977 after preliminary trapping in December 1976 indicated the suitability of the site. Trap stations were placed at 15 m intervals (2.7 ha). The grid was positioned to include portions of three distinct, sharply delineated microhabitats—rocky areas (lajeiros), low thorn scrub, and old field. Trapping was conducted from January 1977 through February 1978. One large Sherman live trap and a larger, wire live trap manufactured in Brazil were set at alternate



Fig. 3.—Map of the Fazenda Batente study area. Unshaded area represents thorn scrub, with exposed rock floors (zig-zagged lines) and major rock formations indicated. Shaded area denotes old field, and the superimposed horizontal lines represent the area covered by a temporary lake. Trap locations are indicated by numbers and letters. Hatched line represents a wooden fence.

stations. Traps were rotated after 3 to 14 days, depending on total number of days trapped each month, capture success, and weather conditions. Capture success was extremely low during the first months, so the planned trapping period of 7 days each month was slowly increased through July, after which traps were set every possible day. Traps were opened just before dusk and checked the following morning. A number of baits (Brazil nuts, peanuts, field corn, pineapple, and other fruits) were used because the availability varied. Total trapping effort during the 14-month study was approximately 25,000 trap nights.

Animals on the grid were toe-clipped when first captured. The in-

formation recorded at each capture included identification number, species, sex, location on grid, weight, and external reproductive status.

Additional information on small mammals was obtained in a variety of ways. Live and kill trapping were conducted at a number of other sites within the municipality of Exu, on the Chapada do Araripe, and elsewhere in the Caatinga; localities and specimens collected are reported in Mares et al. (1981). Trapping sites and collection records of AGGEU (a health agency responsible for monitoring bubonic plague-transmitting ectoparasites on small mammals) were also examined. Finally, captive specimens of most species were maintained for extended periods for behavioral studies.

Vegetation

The characteristics of the vegetation on the grid precluded use of the standard point quarter method (Cottam and Curtis, 1956). The technique was then modified by eliminating consideration of diameter at breast height (DBH), and recording the first plant encountered in each quarter. This modification is more accurate in reflecting the natural state of the vegetation in the thorn scrub and lajeiro microhabitats on the grid while permitting calculation of frequency of occurrence and determination of species composition to be performed in the typical manner. A total of 278 points was examined at 5-m intervals along the grid lines. A foliage height profile was also obtained by assigning the plants examined at each point to one of three foliage height classes: <1 m, 1–3 m, and >3 m. These categories were chosen because the height distribution of Caatinga Baixa plants tends to fall naturally within these divisions.

Climate

Weather records were not available for Exu. The closest station was in Ouricuri, located approximately 60 km to the south. Information on minimum and maximum daily temperatures and precipitation were provided by SUDENE, Divisão de Hidrologia. The area around Exu is somewhat more mesic than that around Ouricuri due to the proximity of Exu to the Chapada do Araripe.

RESULTS AND DISCUSSION

Vegetation

The species composition and frequency of occurrence within each foliage height class are listed in Table 1. A total of 62 species occurred on the grid. Leguminosae and Euphorbiaceae were well represented, with nine and four species, respectively. The 10 most frequently en-

Table 1.—Species composition and frequency of occurrence by foliage height class for *Caatinga* vegetation.

Common name	Scientific name	Family	<1 meter			1–3 meter			>3 meter			Total	
			N	Freq		N	Freq		N	Freq		N	Freq
Marmeleiro	<i>Croton jacobinensis</i>	Euphorbiaceae	49	.191		116	.334		219	.430		384	.345
Canela de nambu	<i>Jacobinia</i> sp.	Acanthaceae	32	.125		53	.153		18	.035		103	.093
Camara	<i>Ruellia paniculata</i> and <i>Ruellia bahiensis</i>	Acanthaceae	18	.070		24	.069		50	.098		92	.083
Feijao de rolinha	<i>Phaseolus peduncularis</i>	Leguminosae	1	.004		2	.006		47	.092		50	.045
Maria preta	<i>Cordia globosa</i>	Boraginaceae	9	.035		27	.078		8	.016		44	.040
Chuchalhode vacuero	<i>Cardiospermum haliacabum</i>	Sapindaceae	6	.023		5	.014		28	.055		39	.035
Moroto		Leguminosae	21	.082		9	.026		5	.010		35	.031
Vrdo	<i>Erythroxylum</i> sp.	Erythroxylaceae	2	.008		12	.035		21	.041		35	.031
Cancasao	<i>Cnidocolus wrens</i>	Euphorbiaceae	18	.070		15	.043		1	.002		34	.031
Lambe bes			11	.043		8	.023		11	.021		30	.027
Frejois			6	.023		1	.003		17	.033		24	.022
Malva	<i>Sida galtheirensis</i>		15	.059		5	.014		1	.002		21	.019
Melosa	<i>Gaya</i> sp.	Malvaceae	12	.047		7	.020		0	.000		19	.017
Bamburra	<i>Blainvillea rhomboidea</i>	Compositae	12	.047		4	.012		0	.000		16	.014
Quichaba			4	.016		6	.017		5	.010		15	.013
Pao moco			1	.004		7	.020		5	.010		13	.012
Catingeira	<i>Caesalpinia pyramidalis</i>	Leguminosae	1	.004		1	.003		11	.021		13	.012
Camara do boi	<i>Ruellia</i> sp.	Acanthaceae	3	.012		6	.017		3	.006		12	.011
Folha de carne	<i>Serjania</i> sp.	Sapindaceae	2	.008		2	.006		8	.016		12	.011
Cipo de cruz			1	.004		2	.006		7	.014		10	.009
Espinheiro branco		Leguminosae	2	.008		2	.006		5	.010		9	.008
Orelha de onca	<i>Cordia insignis</i>	Boraginaceae	1	.004		3	.009		4	.008		8	.007
Manicoba	<i>Manihot</i> sp.	Euphorbiaceae	0	.000		1	.003		7	.014		8	.007
Gtirana	<i>Ipomoea sobrevoluta</i>	Convolvulaceae	1	.004		0	.000		7	.014		8	.007
Rompe-gibao			0	.000		6	.017		0	.000		6	.005
Mucuna	<i>Erythrina velutina</i>	Leguminosae	0	.000		0	.000		5	.010		5	.004
Parreira	<i>Cissis simsiana</i>	Vitaceae	0	.000		0	.000		4	.008		4	.004
Angico marco		Leguminosae	4	.016		0	.000		0	.000		4	.004
Batata de tiu			0	.000		2	.006		2	.004		4	.004
Cipo	<i>Commelina</i> sp.	Commelinaceae	1	.004		2	.006		1	.002		4	.004

Table 1.—Continued.

Common name	Scientific name	Family	<1 meter		1-3 meter		>3 meter		Total	
			N	Freq	N	Freq	N	Freq	N	Freq
Bananinha			3	.012	0	.000	0	.000	3	.003
Juro beba	<i>Solanum paniculatum</i>	Solanaceae	3	.012	0	.000	0	.000	3	.003
Juazeiro	<i>Ziziphus joazeiro</i>	Rhamnaceae	2	.008	1	.003	0	.000	3	.003
Xique-xique	<i>Pilosocereus gounellei</i>	Cactaceae	1	.004	2	.006	0	.000	3	.003
Feijao braba	<i>Capparis</i> sp.	Capparaceae	2	.008	0	.000	0	.000	2	.002
Carrancuro			2	.008	0	.000	0	.000	2	.002
Capim			2	.008	0	.000	0	.000	2	.002
Cordao de Sao Francisco	<i>Leonotis nepetaefolia</i>	Labiatae	0	.000	2	.006	0	.000	2	.002
Canafistula	<i>Cassia excelsa</i>	Leguminosae	0	.000	2	.006	0	.000	2	.002
Chanana	<i>Centratherum punctatum</i>	Compositae	0	.000	2	.006	0	.000	2	.002
Amarra cachorro			1	.004	0	.000	1	.002	2	.002
Espinheiro de algulha			0	.000	2	.006	0	.000	2	.002
Bura leiteira			0	.000	0	.000	2	.004	2	.002
Brao ulna			1	.004	0	.000	0	.000	1	.001
Gini papo			1	.004	0	.000	0	.000	1	.001
Falva			0	.000	0	.000	1	.002	1	.001
Yami			0	.000	1	.003	0	.000	1	.001
Anjico		Leguminosae	0	.000	0	.000	1	.002	1	.001
Velame		Euphorbiaceae	0	.000	1	.003	0	.000	1	.001
Graviola	<i>Croton campestris</i>		0	.000	0	.000	1	.002	1	.001
Pao piranha			0	.000	0	.000	0	.000	0	.000
Mamaozinho			0	.000	1	.003	0	.000	1	.001
Imbu	<i>Amburana cearensis</i>	Leguminosae	0	.000	0	.000	1	.002	1	.001
Pao pretinha			1	.004	0	.000	0	.000	1	.001
Malva preta	<i>Sida peniculata</i>	Malvaceae	1	.004	0	.000	0	.000	1	.001
Aroeira	<i>Astronium urundeuva</i>	Anacardiaceae	0	.000	1	.003	0	.000	1	.001
Ortiga			1	.004	0	.000	0	.000	1	.001
Violette			0	.000	1	.003	0	.000	1	.001
Manda caru	<i>Cereus jamacaru</i>	Cactaceae	0	.000	0	.000	1	.002	1	.001
Capim mimosa	<i>Aristida</i> sp.	Gramineae	0	.000	1	.003	0	.000	1	.001
Maracuja de estrela			1	.004	0	.000	0	.000	1	.001
Totals			256	.230	347	.312	509	.458	1112	

countered plants comprised 76.1% of the vegetation sampled and included five trees, three vines, and two woody shrubs. Marmeleiro (*Croton jacobinensis*) was by far the most abundant plant in all three size classes. The >3 m class constituted 45.8% of the vegetation, the 1–3 m class contributed 31.2%, and the <1 m class comprised only 23.0% of the total. Inclusion of vines in the >3 m class inflated this subtotal but vines were often much longer than 3 meters and substantially increased the density of the canopy. Many produced large quantities of fruits and/or seeds. Of the 10 most abundant plants in the >3 m class, five were trees, four were vines, and one was a shrub; these 10 species constituted 84.2% of the total in that class. In the 1–3 m category, the 10 most abundant plants accounted for 80.1% of the total. The <1 m size class was least common and in part reflects the density of the canopy; the 10 most common species in the lowest layer comprised 76.9% of the total.

Climate

Climatograms (Walter, 1973) portray the relative water balance of an area by plotting mean, monthly maximal temperatures against mean monthly rainfall. When mean monthly rainfall in millimeters exceeds two times the mean monthly maximal temperature in $^{\circ}\text{C}$, a surplus of water is indicated. As the difference between rainfall and temperature increases, so does the relative degree of surplus. Because the measure is a relative one, direct comparisons between areas on the basis of climatograms must be made with caution. Also, climatograms do not take into account any factors other than temperature and rainfall; in the Caatinga, the geological composition compounds the degree of water deficit.

Mean monthly rainfall and mean, maximum monthly temperature for the period of September 1964 through August 1978 are plotted in Fig. 4 in the form of a modified climatogram. Monthly averages are used to illustrate the relative abundance or paucity of water in a given region. Mean values alone, however, may be misleading when variability is high within the system. The enormous variability in rainfall is depicted in Fig. 5; the months of June, July, August, and September consistently experience substantial water deficits but the other months are more variable. A summary of the occurrence of water deficits and surpluses is presented in Table 2. The water surpluses which occur approximately 50% of the time in December and January, and less frequently in November, are produced by the erratic advances of the continental equatorial air mass which sometimes penetrates as far east as the middle of the São Francisco River basin (Reis, 1976). Sufficient precipitation to produce a water surplus is most likely to fall in March and April, but this failed to occur 20% and 35% of the time, respec-

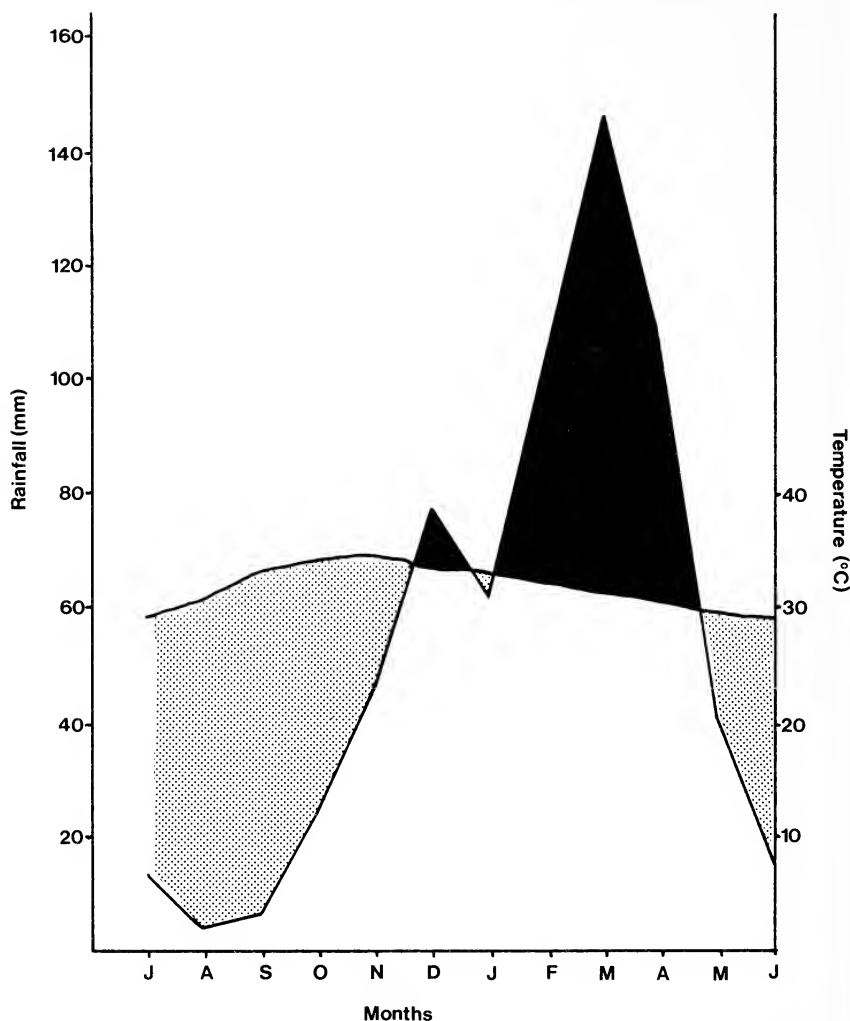


Fig. 4.—Modified temperature (mean of average maximum monthly temperature in °C)-rainfall (mean total monthly rainfall in mm) climatogram for the 14-year period, September 1964–July 1978. Light shading indicates periods of relative water deficit; dark shading represents relative water surplus.

tively, between 1964 and 1978. Water surpluses also occurred approximately one-half (57%) of the time in February and approximately one-third (36%) of the time in May. Precipitation in these months is generated by the Intertropical Convergence Zone and generally constitutes the bulk of the annual rainfall, although quantities vary greatly

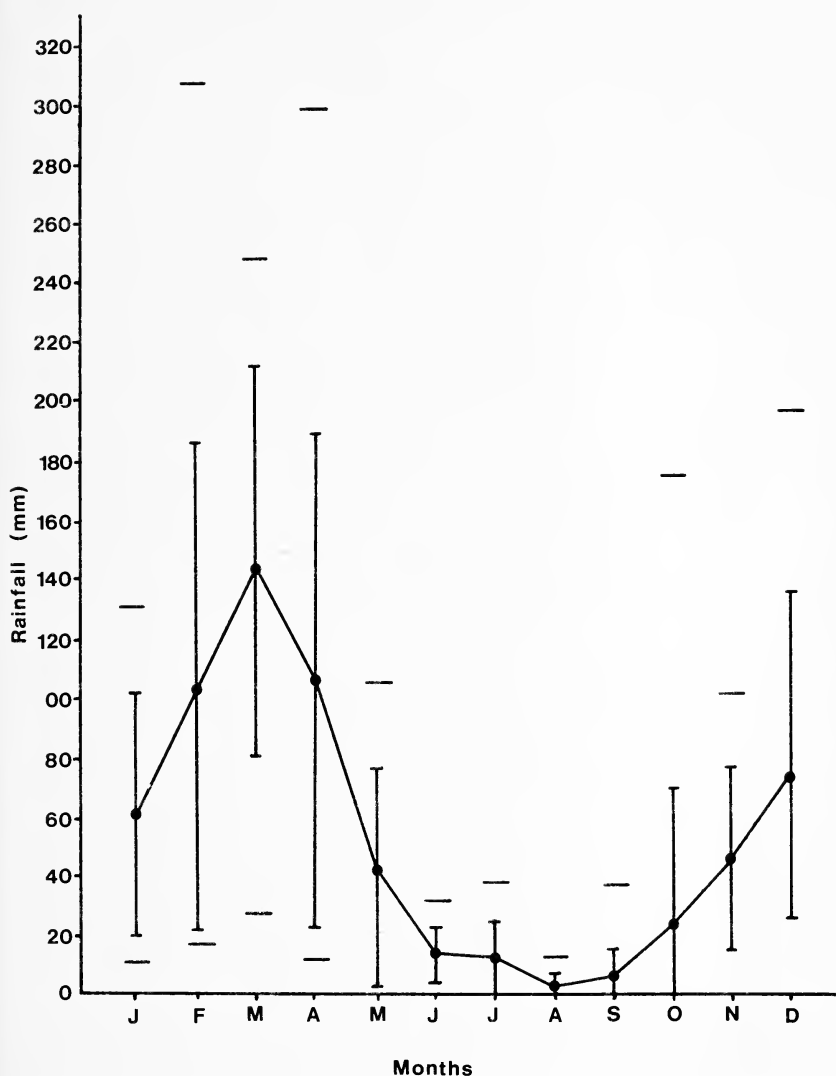


Fig. 5.—Mean monthly rainfall (mm) recorded at the SUDENE weather station in Ouricuri, Pernambuco. Vertical bar indicates \pm standard deviation; horizontal lines show the range.

among months and between years. The wide range of conditions produced by the unpredictable rainfall in the Caatinga is obscured when mean values only are used. Therefore, modified climatograms were constructed for each year to illustrate the conditions which must be

Table 2.—*Monthly occurrence of water deficits¹ and surpluses between September 1964 and August 1978.*

Month	Number of months with water surpluses	%	Number of months with water deficits	%
January	6	42.9	8	57.1
February	8	57.1	6	42.9
March	11	78.6	3	21.4
April	9	64.3	5	35.7
May	5	35.7	9	64.3
June	0	00.0	14	100.0
July	0	00.0	14	100.0
August	0	00.0	14	100.0
September	0	00.0	14	100.0
October	1	7.1	13	92.9
November	4	28.6	10	71.4
December	7	50.0	7	50.0

¹ Deficits occurred when \bar{x} monthly temperature $^{\circ}\text{C} > \frac{1}{2} \times \text{mm rainfall per month}$ (Walter, 1973).

dealt with by the fauna. This relatively short 14-year period encompassed intervals of highly concentrated, abundant rainfall, such as those in 1966–1968, and intervals of prolonged water deficit, such as the span from May 1975 to February 1976 (Fig. 6).

The temperature regime is relatively stable within and between years in comparison to the rainfall regime. Mean monthly maxima generally vary only 7–8 $^{\circ}\text{C}$ on an annual basis and mean monthly minima generally vary only 5–6 $^{\circ}\text{C}$. Monthly maxima temperature averages for the period of September 1964 through August 1978 are plotted in Fig. 6.

SPECIES ACCOUNTS

Order Marsupialia

Family Didelphidae

Monodelphis domestica (Wagner, 1842)

short bare-tailed opossum; catita

Monodelphis domestica ranges throughout much of northeastern Brazil. Catitas may be found in most habitats but are most abundant on the various types of granitic outcroppings. These small marsupials are basically nocturnal, with peak activity occurring just after dusk. Catitas are primarily terrestrial but are also adept climbers.

Catitas are very efficient predators, concentrating on invertebrates in the field. Small vertebrates, including frogs, lizards, snakes, and mice were readily accepted as food items by laboratory specimens. A 20-g subadult is capable of subduing and killing a 15-g lizard. The

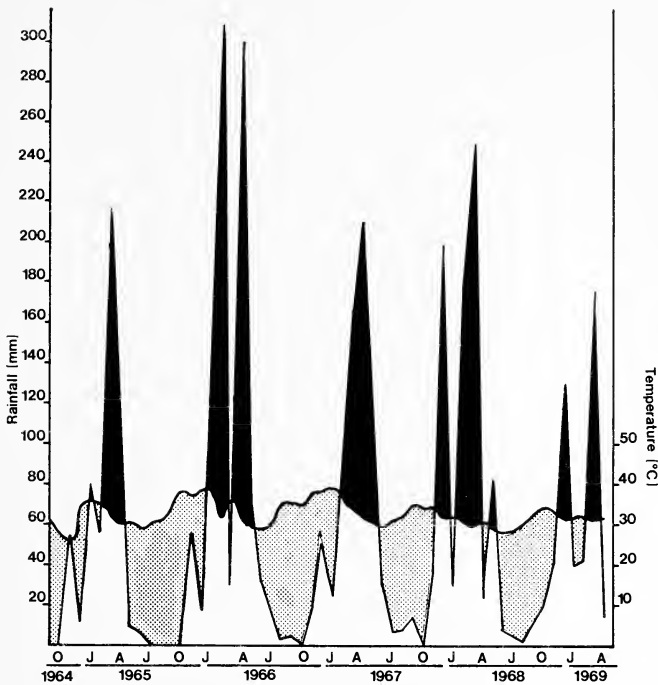


Fig. 6A.—Modified temperature (mean maximum monthly temperature in °C)—rainfall (total monthly rainfall in mm) climatogram for the 14-year period, September 1965–July 1978. Shading as in Fig. 4.

manipulative skill of the forepaws is also pronounced; catitas can snatch up small ants with ease and grab flying insects from the air. Wild caught individuals were also presented with numerous types of invertebrates. The manipulation of scorpions is particularly interesting; the animal approaches slowly, then lunges and pins the scorpion to the ground with the forefeet. It then bites off the last few segments on the tail and proceeds to eat the now harmless scorpion, beginning with the head and working back to the tail, removing the appendages in the process. When catitas are eating, they are oblivious to external disturbances, including agonistic threats by other individuals.

Reproduction occurs throughout much of the year in the field. Litter size ranges from one to 11 altricial young which are not protected by a marsupium. Single family groups were often maintained in captivity for extended periods of time with minimal fighting between individuals.

Monodelphis domestica is generally difficult to trap. They are rela-

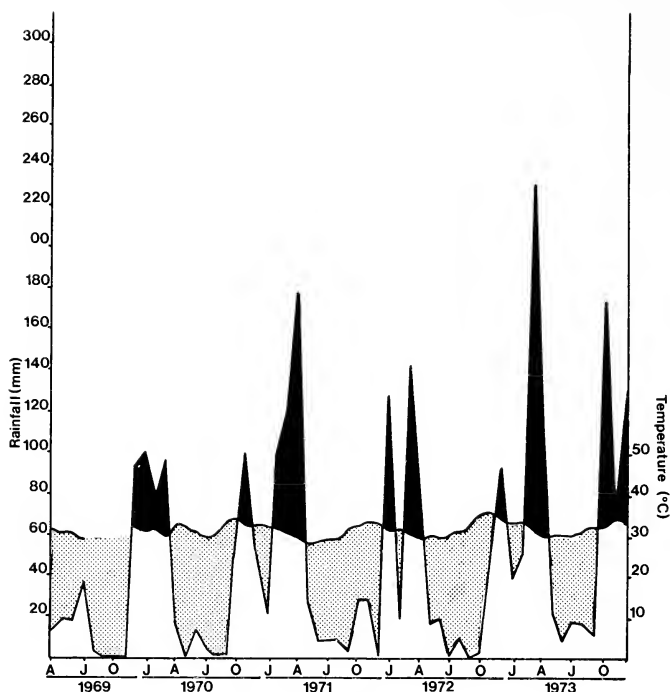


Fig. 6B.

tively docile and seldom attempt to bite. Upon release from traps or after handling, many individuals foraged as they moved away from the trap station. Much of their behavior is similar to that observed for *D. albiventris*.

Marmosa karimii Petter, 1968

Very little is known about this species. No information is available on macrodistribution or patterns of reproduction. It appears to be very rare; part-time collectors were offered a reward equal to the minimum daily wage for a farm hand for each animal caught, so the incentive was high, but only two specimens were captured. These were maintained in the laboratory on a diet of insects, beef, and fruit. Captive specimens were extremely timid and difficult to observe without disrupting their activity. The amount of time spent climbing or perched above the cage floor indicated a high degree of arboreal activity in this species. Flying insects were snatched in mid-flight and manipulated by the forefeet while the prehensile tail and hind limbs supported the body.

Casacas are opportunistic feeders. Scats of free ranging opossums, however, typically consisted almost exclusively of the seeds of whatever fruit happened to be locally abundant. Invertebrate remains, especially those of beetles, centipedes, and scorpions, were also found in scats or in examinations of stomach contents. Laboratory specimens accepted a wide variety of food items, including live frogs and lizards, the carcasses of rodents and snakes, most native and domestic fruits, and various invertebrates.

These opossums are, in general, relatively timid, docile animals. Most of the time, the bared teeth, snarling, hissing, and screeching constitute an elaborate bluff. Handling rarely presented problems, as many individuals entered a state similar to death feigning, though not quite as pronounced. Upon release, very few individuals climbed, even though trees were available; typically, released individuals headed for rocks and wedged themselves into a crack between or under large rocks or boulders. Cracks and fissures were also used as nest sites, with certain preferred locations being consistently utilized, although by different individuals. In general, the behavioral repertoire of *D. albiventris* is very similar to that described for *D. virginiana* by McManus (1970).

Order Rodentia
Family Muridae
Subfamily Cricetinae
Oryzomys eliurus Wagner, 1845
rice rats; ratinha da cana

Vieira (1955) reported the distribution of *O. eliurus* as ranging from southern Mato Grosso, Minas Gerais, and Bahía, to the state of Paraná. In the area around Exu, this mouse is only found relatively close to the base of the Chapada do Araripe. The Cerrado vegetation on the top of this plateau has apparently served as an invasion corridor; *O. eliurus* is more common on the more mesic northern slope and top of the chapada. The only microhabitats occupied by this species near Exu are cultivated fields and recently abandoned fields.

Oryzomys subflavus Wagner, 1842
rice rats; rato da cana

The distribution includes northern and northeastern Brazil to the state of Minas Gerais (Vieira, 1955). This species is essentially commensal in the area around Exu and is restricted to sugar cane fields and occasionally other cultivated fields near the base of the Chapada do Araripe. *Oryzomys subflavus* is another species common in the Cerrado which is a marginal inhabitant of the Caatinga and can only exist in the more mesic locales near the chapada.

Bolomys lasiurus (Lund, 1841)
rato do campo; pixuna

This animal was formerly recognized as *Zygodontomys pixuna* Moojen but has recently been classified by Reig (1978) as *Bolomys lasiurus*. Moojen (1952) listed the geographic distribution of *Zygodontomys pixuna* in Brazil as the states of Ceará and Pernambuco. Individuals were found only in cultivated fields and in abandoned fields in early seral stages of old field succession. Other habitats may be occupied to some extent during population eruptions. *Bolomys* thus appears to be dependent on slash and burn agricultural habitat. Naturally occurring fires could conceivably produce the same results but are less predictable and widespread.

B. lasiurus is primarily nocturnal and terrestrial. Laboratory specimens were occasionally active for brief periods during the day, generally during morning hours. Captive individuals exhibited very little inclination or ability to climb. Pixunas are microomnivores.

Most of the females captured in April, May, and June by Karimi et al. (1976) were pregnant; population density subsequently peaked in July, August, and September. Population density as high as 187 individuals/ha was observed in June and July.

This species constructs nests of finely woven, shredded grass and leaves. Karimi et al. (1976) excavated a number of burrow systems; these generally have two to five openings, with a long, shallow tunnel leading down into a chamber lined with finely shredded material. More elaborate systems have two branching tunnels leading into a spherical chamber 15 to 20 cm in diameter and approximately 40 cm below the surface. If soil conditions were suitable, Karimi et al. (1976) found that animals placed in terrariums immediately dug out nests; with poor soil conditions, surface nests were constructed but hidden under grass.

Individuals were often relatively docile when handled. When released from traps, their escape behavior usually consisted of rapid, weaving movements into progressively thicker vegetation.

Calomys callosus Rengger, 1830
vesper mouse; rato pequeno

Calomys has a broad geographic distribution, including eastern Brazil; forest fringes and scrublands in southern Brazil, Paraguay, and the Bolivian Chaco; the plains of northern Argentina; and the eastern Andean slopes between La Paz, Bolivia, and Córdoba in Argentina (Hershkovitz, 1962). In the Caatinga, *C. callosus* was found only in the latter seral stages of old field succession and Caatinga Baixa habitats.

Calomys callosus is an active, agile climber. The long tail is used as a climbing aid. A pronounced inclination toward arboreal activity was

observed in the laboratory. In the field, this species probably spends as much or more time foraging in trees and shrubs as it does on the ground. Adults are capable of sheer vertical leaps of approximately 0.7 to 0.8 m.

These animals were strictly nocturnal in the laboratory and quite easily maintained. They accepted most native seeds offered to them, but appeared to prefer the seeds of an unidentified legume common in open thorn scrub formations and the seeds of various grasses. Moths and beetles were also highly preferred food items. Nests constructed in the laboratory were essentially spherical in shape and consisted of finely shredded, interwoven plant material. This sort of material also lined the nests found in the field, but these were simple depressions hollowed into the ground, approximately 10 to 15 cm in depth and width and camouflaged with twigs and leaves. A few nests were found under thin, flat rocks or roofing tiles. These systems were a bit more complex and had two or more openings; occasionally, small stores of seeds would be located a short distance from the central nest.

Calomys were never found in large numbers and were generally uncommon. Karimi et al. (1976) reported a similar conclusion.

Mello (1977a, 1978b) presented information on their general biology and reproduction in the laboratory. The mean litter size was reported to be 4.5 (Mello, 1977b) and the range was from two to nine (Mello, 1978). This species has a postpartum estrous and a mean gestation period of 21.8 days (Mello, 1977b). The short gestation period, relatively large litter size, and postpartum estrous create a high reproductive potential.

Calomys are typically docile animals. The basic response to being startled or handled is to "freeze" in position and remain motionless. This behavior also functions in predator avoidance; when motionless, *Calomys* are essentially indistinguishable from the ground litter.

Wiedomys pyrrhorhinos (Wied, 1821)

red-nosed mouse; rato vermelho

The distribution of *Wiedomys pyrrhorhinos* in Brazil includes the states of Ceará, Pernambuco, Paraíba, Bahia, Minas Gerais, northern Mato Grosso, Paraná, and Rio Grande do Sul (Moojen, 1952). In the Caatinga, *W. pyrrhorhinos* was trapped only in Caatinga Baixa formations.

These nocturnal rodents are deft climbers and make extensive use of their long tails for balance. Laboratory animals spent a great deal of time climbing about the cages. Nests are typically placed above ground in trees or shrubs. One pregnant female was observed in an abandoned bird nest situated in a cansação (*Cnidocolus wrens*); these

plants are protected by spines covered with compounds exceedingly irritating to humans and presumably other animals. Moojen (1952) listed a number of objects used as nest sites, including holes in trees, parakeet-excavated termite mounds, and abandoned bird nests.

Litter size ranges from one to six altricial young. Lactating females readily adopt other young; one female successively nursed her own litter, a litter of *Calomys*, and a *Bolomys* litter. One pregnant female that was collected still had a subadult pelage.

This species was never abundant at any locale. Food items accepted by laboratory specimens included most native seeds. They avidly chased and ate beetles and moths in the laboratory, but were relatively inefficient predators. No evidence of food storage was observed. In general, these animals are timid and difficult to handle.

Family Caviidae

Kerodon rupestris (Wied, 1820)

rock cavy; mocó

The distribution in Brazil includes the northeastern states and portions of Bahia and Minas Gerais (Moojen, 1952). Mocós are generally restricted to structurally diverse rocky areas, especially serrates and serras, but often occupy lowland lajeiros. *Kerodon* are subject to intense hunting pressure because they are large rodents with high quality flesh (Lacher, 1979), the stomach is prized as a starter for cheese, and certain behavioral traits make them easy prey for hunters. This species' practice of defecating on the same elevated locations, and characteristic alarm call (the call itself bounces off the rocks, making it difficult to locate the source) confirms its presence.

Mocós are extremely agile animals. The leathery pads on the feet are used to great advantage as they maneuver in the rocks, often bounding or ricocheting from boulder to boulder. They are also deft climbers and obtain most of their sustenance by foraging in tree tops. They frequently leap straight to the ground if startled while foraging.

Mocós use rock fissures or the cracks beneath boulders as nest sites and refugia from predation, wedging their bodies into narrow cracks when pursued. Females reproduced year-round under laboratory conditions, with a litter size of one or two young (Lacher, 1980); the young are very precocial.

At times, as many as four or five individuals could be observed moving about the rocks during the day on a small but complex section of the grid, but only five individuals were captured in 25,000 trap nights on the grid. These animals were relatively docile, easily handled animals and never attempted to bite.

There is some potential for domestication (Lacher, 1979).

Galea spixii (Wagler, 1831)
cavy; preá

Galea spixii has a wide distribution in Brazil, ranging throughout the Northeast, in the states of Bahía, Goias, Mato Grosso, and Minas Gerais (Moojen, 1952). In the Caatinga, preás were found in most lowland habitats, especially in recently abandoned and cultivated fields. This cavy is tailless, terrestrial, and primarily diurnal, but is also active for short intervals during the night.

Reproduction occurred throughout the year and females were capable of producing several litters annually. Litter size ranged from one to five. The young are precocial but to a lesser degree than either *K. rupestris* or *T. apereoides*.

Galea spixii is the only Caatinga rodent which develops and consistently utilizes a network of runways. Areas frequented by preás were readily distinguished by the presence of runways and numerous small cleared patches used for sandbathing. Nest sites appeared to be temporary and are typically located under rocks or low, overhanging vegetation. Acceptable food items included most types of vegetation; *G. spixii* is strictly herbivorous.

Preás were often relatively difficult to capture unless traps were placed squarely in runways. The adherence to these familiar pathways is best illustrated by several incidents where *G. spixii* was spotted running under a boulder or into thick vegetation; an open live trap was then placed on the just-used runway and the hiding place approached from the other side. Each individual ran back along the entry route and into the trap, sometimes banging repeatedly against the back of the trap until it closed. This occurred even though the traps were plainly visible for 4 or 5 m at ground level and were easily avoidable.

Behavior in traps was quite variable, but a large portion of first-capture animals completely wore the fur off their snouts by constantly butting the sides of the trap. Some individuals continued to exhibit this behavior upon subsequent recaptures. Many preás struggled and kicked extensively when first handled, but during hundreds of handling bouts of live-trapped and laboratory animals, none attempted to bite. Preás frequently displayed a behavior similar to death feigning by opossums; when handled, the body became limp until deposited on the ground. This state sometimes persisted for several minutes beyond the completion of handling procedures.

Family Dasyproctidae
Dasyprocta prymnolopha (Wagler, 1831)
agouti; cotia

Cotias range in Brazil from the state of Pará to southern Brazil (Moojen, 1952). They were apparently quite abundant in the past on

the granitic outcroppings, but widespread habitat destruction and intense hunting pressure have extirpated them from most locales. Currently, cotias are restricted to patches of High Caatinga vegetation and isolated serrotes in much of the Caatinga. These animals apparently feed primarily on fruits and larger seeds.

Family Echimyidae

Thrichomys apereoides (Lund, 1841)

spineless spiny rat; punaré

The two species in the genus range throughout eastern and central Brazil and Paraguay (Walker, 1975). In the Caatinga punarés are found only in the granitic formations, including lowland lajeiros and elevated serrotes and serras. This strict association with rocky habitat is also characteristic of populations in the very mesic, remnant Atlantic Forest. Populations in the Cerrado are also restricted to isolated rocky areas (T. E. Lacher, Jr., personal communication). Echimyids typically occupy relatively mesic habitats, and most die when exposed to heat and dryness (Walker, 1975); thus *T. apereoides* is somewhat of an exception within the family.

This species is very agile and quite adept at maneuvering in structurally diverse, boulder strewn locales. Nests are typically situated under large boulders when available. The numerous cracks and crevices produced by the splitting and exfoliation of the granitic rock serve as temporary refuges. Individuals are difficult to dislodge when wedged into narrow cracks. Animals which escaped from cages were generally found jammed behind an object leaning against a wall.

Punarés tended to be active for short periods both day and night but exhibited definite crepuscular peaks in activity. They may perhaps be best classified as semiarboreal. Individuals were capable of traversing branches less than one-half centimeter in diameter with ease. The long, heavy tail was used extensively as a pendulum-like counterbalance while climbing and also served as the third leg of a tripod during the stereotyped, upright postures characteristic of agonistic behavior. Paradoxically, for such an important appendage the tail is easily fractured and portions are readily lost, as is the case with most other echimyid species (Walker, 1975). Adults grabbed by the tail leap forward and up into the air, executing a 360° side-to-side twisting of the body which autotomizes the tail at the point of contact or near the base; juveniles less than 12 hrs old have also been observed to attempt this maneuver.

Litter size ranged from one to six. The young are very precocial and often begin to eat solid foods on the day of birth. Grooming behavior is also initiated shortly after birth. Nursing frequently continued until the young weighed 50 to 60 g, but young as light as 15 to 20 g survived in the laboratory without nursing.

Table 3.—General distribution patterns of small mammals in the Caatinga and adjacent biomes. W = widespread, L = limited distribution, A = absent, ? = unknown or uncertain.

Species	Cerrado	Caatinga	Atlantic Rainforest
Marsupialia			
Didelphidae			
<i>Monodelphis domestica</i>	W	W	W
<i>Marmosa karimii</i> ¹	L?	W?	?
<i>Didelphis albiventris</i>	W	W	W
Rodentia			
Muridae			
<i>Oryzomys eliurus</i>	W	L	A
<i>Oryzomys subflavus</i>	W	L	A
<i>Bolomys lasiurus</i>	W	L	?
<i>Calomys callosus</i>	W	L	A
<i>Wiedomys pyrrhorhinos</i>	L	W	A
Dasyproctidae			
<i>Dasyprocta prymnolopha</i> ¹	A?	W?	A?
Caviidae			
<i>Kerodon rupestris</i> ²	L	W	A
<i>Galea spixii</i>	W	W	W?
Echimyidae			
<i>Thrichomys apereoides</i> ²	L	W	L

¹ Distributional patterns not well established.

² Limited to rocky habitats in areas of occurrence.

Laboratory specimens accepted essentially every type of native seed offered, including many from legumes. Insects, particularly beetles and moths, were quickly ingested. In general, food items less than 2 mm in length were not manipulated with the forepaws.

Punarés, especially subadults, are relatively easy to capture during dry periods. Adults tended to avoid traps in wet periods, but subadults remained very susceptible. Individuals caught for the first time were generally quite vocal and prone to struggle extensively when handled, but rarely attempted to bite. Most individuals became increasingly docile with subsequent recaptures.

DISCUSSION

The terrestrial small mammal fauna in this portion of the Caatinga consisted of 12 species. Rodents were represented by nine species in four families and marsupials by three species in a single family. Two other rodents, *Mus musculus* and *Rattus rattus*, were also present but

occur only in buildings. Additional information on the mammal fauna of the Caatinga can be found in Mares et al. (1981).

Most of the small mammal species have relatively broad geographic distributions in South America, extending far beyond the boundaries of the Caatinga. Hershkovitz (1972) has previously noted the low degree of endemism in the Caatinga. Approximately 50% of the species found in the Caatinga also occur in the Atlantic Rainforest (Table 3). The degree of overlap with the Cerrado is even greater; approximately 90% of the species are present in both biomes, however, eight of the 11 shared species have very limited distributions in one or the other biome. The fauna of the Caatinga is, in general, mainly composed of species that occur throughout the open formations (Vanzolini, 1973) that dominate central South America.

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ARTICLE 6

ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA. II. WATER RELATIONS

KARL E. STREILEIN¹



ABSTRACT

Small mammal species from the semiarid Caatinga of Brazil do not possess pronounced physiological capabilities for water conservation. The granitic outcroppings distributed throughout this xeric region serve as "microrefugia," thus most of the cavimorph rodent and marsupial species are able to compensate for a low degree of physiological capabilities by preferentially utilizing the relatively mesic, rocky habitats; none of the murid rodents exhibit this behavior.

INTRODUCTION

Literature Review

Water is the ultimate limiting factor for many vertebrate species in xeric regions. Volant forms such as birds and bats are able to traverse long distances in search of free water, but this strategy is not feasible for small terrestrial mammals. It has long been apparent to zoogeographers that xeric zones, particularly deserts, frequently function as geographic barriers or filter zones with respect to most small mammals. Given the restrictive physical factors and basic morphological constraints of the animals, it would appear that the number of possible strategies is limited and that a great deal of time for adaptation or preadaptation may be necessary before the required elements may be evolved (Mares, 1973, 1976).

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The particular suites of attributes characteristic of various xeric-adapted species may best be viewed with respect to their functional position along a gradient of high-low availability of water (Mares, 1975). Simple behavioral traits, such as selection of a relatively mesic microhabitat in an otherwise xeric area or selection of water-rich foods, may suffice to maintain a positive water balance. Some desert-dwelling species of the genera *Neotoma* and *Peromyscus* (MacMillen, 1964) in North America and *Microcavia* (Mares, 1973) in the Monte Desert in Argentina are able to exist in this manner. The probability of incurring a severe water deficit rises greatly as distance from mesic microhabitats increases; correspondingly, behavioral traits tend to increase in number and complexity (Mares, 1976). The behavioral repertoire for water conservation often includes nocturnality, shifting activity patterns in response to variation in microclimatic conditions, burrow plugging, and food storage in relatively moist underground chambers. A very complex and apparently unique behavior which increases the availability of water rather than conserving it is performed by *Leggadina hermannsburgensis*. This Australian murid rodent builds low mounds of pebbles over its burrow systems which function as dew-traps (Walker, 1975).

Physiological capabilities for water conservation also tend to increase in conjunction with the expansion of the behavioral repertoire. Typical conservation techniques include urine concentration, recycling of metabolic water, torpor, and others (Schmidt-Nielsen, 1964). In some instances, combinations of behavioral traits and physiological attributes allow species to exist totally independent of free water.

Highly adapted rodent species (for example, those which can exist without free water) are known from many of the deserts of the world, including Mexico, the United States, Egypt, India, and Australia (Mares, 1973). There are only two South American species, *Phyllotis gerbillus* (Koford, 1968) and *Calomys musculus* (Mares, 1977c), known to be independent of free water. With the exception of the physiological studies conducted by Mares (1973, 1975, 1977a, 1977b, 1977c, 1977d) on the rodents of the Monte Desert, very little information is available on the physiological capabilities of the fauna in other South American xeric zones.

South America has quite a variety of xeric regions, including the Atacama and Sechura Deserts on the western coast, the Monte Desert and semiarid Patagonian region in Argentina, the semiarid Chaco in Paraguay, Bolivia and Argentina, the Andean Puna, and the semiarid Caatinga in Brazil (Walter, 1973; Cabrera and Willink, 1973). Even though substantial differences exist within this assemblage with respect to area encompassed, amount of rainfall, temperature regime, and floral and faunal composition, the Caatinga stands out because its

rainfall patterns, unlike those in the other regions, are characteristically unpredictable with regard to both amount and timing of precipitation.

The Caatinga

The physiography, climate, and vegetation of the Caatinga, particularly the area near Exu, Pernambuco, in which this study was conducted, were described in an earlier report (Streilein, 1982a). An abbreviated description follows.

Three major geological features typify the Caatinga. Extensive flats of Precambrian crystalline rock dominate the region. The relatively uniform flats are punctuated by widely distributed, structurally complex granitic outcroppings and in a few areas, the surface layer of sedimentary rock (primarily sandstone) has remained intact. Structural diversity in the Caatinga on both the geographic and local scales is thus primarily determined by the number, types, and distributional patterns of granitic formations.

The predominant form of vegetation in the region is Caatinga Baixa, which includes the various types of low thorn scrub with canopy elements rarely exceeding 5 m. Plant species characteristic of a certain type of Caatinga Baixa vegetation may include representatives of the cacti, euphorbs, and/or legumes. In somewhat more mesic locales within the region, low thorn scrub is replaced by Caatinga Alta vegetation, characterized by the presence of large xerophyllic trees (>5 m). Finally, sites that receive substantial orographic rainfall, such as elevated granitic outcroppings and sandstone plateaus, support humid forest.

The climate of the Caatinga is unique with respect to other tropical biomes in South America. Most of the tropics is relatively mesic and seasonally predictable while the Caatinga is semiarid and has an unpredictable rainfall regime. The extreme variability in rainfall patterns produces extended droughts and flooding at irregular intervals. The radical climatic fluctuations thus impose severe constraints upon the small mammal fauna in the region.

Purpose

The primary objective was to examine the water conservation capabilities of Caatinga species in order to determine if the degree of physiological adaptation was correlated with observed distributional patterns. Low population levels in several species, however, eliminated the possibility of examining every species. One representative species was chosen from each of the three general types of habitat utilizers (Streilein, 1982c)—*Thrichomys apereoides*, from the obligate rock dwellers; *Galea spixii*, from the ubiquitous species; and *Bolomys*

Table 1.—Total number, mean initial weight, and standard deviation of the various Brazilian rodent species used in the water deprivation experiments.

Species	Total number ¹	Mean initial weight	Standard deviation
<i>Galea spixii</i>	34	326.2	59.9
<i>Thrichomys apereoides</i>	34	226.8	33.8
<i>Bolomys lasiurus</i>	40	41.5	7.4

¹ Equal sex ratios were used for all experiments.

lasiurus, from the rock avoiders. Water deprivation experiments were then conducted on these species. A variety of reasons prompted the choice of deprivation experiments—the procedures were simple and required no sophisticated equipment; relative weight loss and survivorship could be statistically compared within and among species; and total deprivation possibly approaches natural conditions during extended droughts, thus providing a measure of potential survivorship. *Opuntia* was tested for its utility as an alternate water source for all three species because it is commonly associated with rocky locales.

The apparent inability of *G. spixii* and *B. lasiurus* to maintain elevated populations in the more xeric habitats (Streilein, 1982b) and the strict adherence of *T. apereoides* to the most mesic habitats were used as a basis for three predictions on the outcome of the experiments. First, none of the species were expected to prove to be independent of free water. Second, all three species were expected to exhibit relatively poor water conservation capabilities. Finally, it was thought that the cactus, *Opuntia palmadora*, would be an acceptable alternate water source for *T. apereoides* and perhaps *G. spixii*, but would probably be unsuitable for *B. lasiurus*.

MATERIALS AND METHODS

Laboratory Procedure

Experimental animals.—All specimens were captured within 6 km of Exu, Pernambuco, and were maintained in the laboratory for at least three weeks prior to the initiation of the experiments. Species utilized and the numbers, sex, and mean initial weight (\pm one SD) are listed for each experiment in Table 1. Prior to the initiation of the experiments, *Galea spixii* were maintained on a diet of freshly cut, green grass. *Thrichomys apereoides* and *Bolomys lasiurus* occasionally received canary seed, Brazil nuts, or naturally occurring seeds to supplement their basic staple of field corn. All three species had unrestricted access to water during this period.

Laboratory conditions.—Specimens were housed individually in wire cages with a minimum floor space of 625 cm². Controlled-environment facilities were not available. The laboratory building moderated ambient conditions somewhat, thus the experimental animals were exposed to the natural photoperiod and subjected to temperatures which approximated the mean, maximal daily temperature of 30.2°C (\pm 1.6; range, 27.1–32.6)

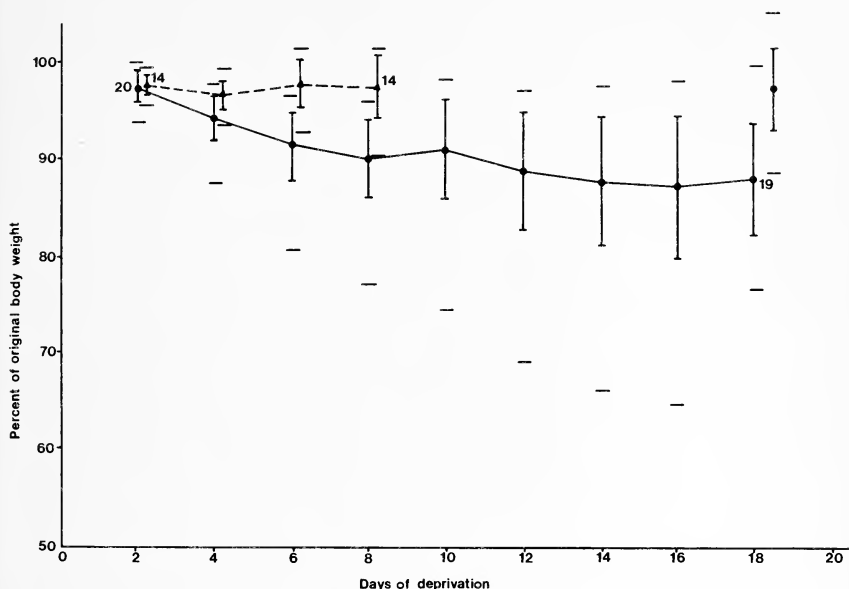


Fig. 1.—Weight response (expressed as percent of initial weight) of *Thrichomys apereoides* during water deprivation experiments. Solid line indicates animals fed corn only, dashed line represents a diet of corn and *Opuntia*. Vertical bar indicates ± 1 SD; horizontal lines show the range. Number of surviving animals are indicated by Arabic numbers adjacent to data points.

and the mean, minimal daily temperature of 20.4°C (± 1.6 ; range, 17.6–22.3) recorded at the nearest weather station.

Weight monitoring.—All individuals were weighed to the nearest 1.0 g on a triple beam balance at the initiation of an experiment and every other day thereafter until the experiment was terminated or until the animal died, in which case the weight at death was recorded immediately upon discovery. Weights were checked on alternate days to minimize handling-induced stress and the possibility of injury. In order to decrease the disruption of typical daily patterns of activity, weights were taken in the early evening when the animals are normally most active. Injured animals were excluded from the calculations.

Experimental Design

Experiment 1—Water deprivation.—Food was provided *ad libitum* for all three species. *Galea spixii* was given the same grass as that fed prior to the experiment, but after it had been air dried for several weeks; no attempt was made to correlate the amount of water present in the dried grass with changes in humidity. *Bolomys lasiurus* and *Thrichomys apereoides* were provided with sun-dried field corn. The experiment was terminated after 18 days. The only species with a large

Table 2.—Mean percent change in initial body weight for animals deprived of free water. Arcsine transformed data. Sample size in (). Actual means in [].

Species	Treatments	\bar{x}_1	\bar{x}_2	s_1^2	s_2^2	C	P	
<i>Thrichomys apereoides</i>	corn only, males vs females	19.18 [11.2] (10♂)	17.16 [8.9] (10♀)	7.82	17.93	1.26	>.05	ns
	corn and <i>opuntia</i> , males vs females	2.37 [1.0] (7♂)	9.84 [4.1] (7♀)	77.99	62.34	1.67	>.05	ns
	corn only vs corn and <i>opuntia</i>	18.17 [10.0] (20)	6.11 [2.5] (14)	74.09	12.61	4.96	<.001	
<i>Bolomys lasiurus</i>	corn only, males vs females	30.29 [26.6] (7♂)	33.43 [30.5] (10♀)	15.42	9.04	1.78	>.05	ns
	corn only vs corn and <i>opuntia</i>	32.14 [17.7] (17)	24.84 [2.8] (6)	14.05	1.30	7.16	<.001	
	corn only vs corn and grass	32.14 [14.3] (17)	21.55 [67.7] (7)	14.05	37.70	4.25	.01 > P > .001	

number of survivors, *T. apereoides*, was then given access to water for 12 hrs and weighed again the following morning.

Experiment 2—Alternate water sources.—The basic regime described for each species in Experiment 1 was followed. All three species were also supplied with cactus pads (*Opuntia palmadora*). In addition, a separate sample of *B. lasiurus* was provided with freshly cut grass. Fresh cactus pads were split lengthwise and placed in the cages each morning and evening and replenished as needed throughout the day. *Thrichomys apereoides*, and especially *Galea spixii*, typically consumed several pads each day. The second group of *Bolomys lasiurus* received freshly cut grass in the morning and the excess of the previous day was removed; this prevented the animals from constructing nests and thereby ameliorating ambient conditions.

Statistical analyses.—Adjusted t-tests were used to compare mean percent change in body weight over time, percent weight loss at death, average number of days to death, and average number of days survived between sexes within species and among species. Unequal sample variances mandated the use of adjusted t-tests (Armitage, 1971). Percent body weight loss data were arcsine transformed (Sokal and Rohlf, 1969).

Table 3.—Mean number of days survived by animals deprived of free water. Sample size in ().

Species	Treatments	\bar{x}_1	\bar{x}_2	s_1^2	s_2^2	C	P	
<i>Thrichomys apereoides</i>	corn only, males vs females	17.8 (10♂)	18.0 (10♀)	0.36	0.00	1.05	>.05	ns
	corn and <i>opuntia</i> , males vs females	8.0 (7♂)	8.0 (7♀)	0.00	0.00	—	>.05	ns
	corn vs corn and <i>opuntia</i>	8.0 (20)	8.0 (14)	0.00	0.00	—	>.05	ns
<i>Bolomys lasiurus</i>	corn only, males vs females	10.8 (9♂)	10.8 (10♀)	28.95	7.96	—	>.05	ns
	corn vs corn and grass	7.6 (19)	8.0 (7)	1.36	0.00	1.49	>.05	ns
	corn vs corn and <i>opuntia</i>	7.6 (19)	7.1 (9)	1.36	2.11	0.90	>.05	ns
<i>Galea spixii</i>	grass only, males vs females	4.3 (10♂)	5.3 (10♀)	1.34	3.34	1.46	>.05	ns
	grass and <i>opuntia</i> , males vs females	5.6 (7♂)	6.4 (7♀)	0.29	2.62	1.48	>.05	ns
	grass vs grass and <i>opuntia</i>	4.8 (20)	6.0 (14)	2.48	1.54	2.48	<.05	

RESULTS AND DISCUSSION

Thrichomys apereoides

There was no significant difference in percent body weight change between males and females maintained solely on the sun-dried field corn. At the end of the 18-day deprivation period, the 19 surviving individuals had lost, on the average, only 12.0% of their original weight (Fig. 1). Of the 19 survivors, about one-quarter had been slowly regaining weight, approximately one-half had stabilized or were losing less than .005% per day, and the remaining individuals continued to steadily lose weight. This ability to withstand total water deprivation was unexpected in light of this species' strict adherence to the relatively mesic rocky areas. *Thrichomys apereoides* and *Neotoma* in North America had at first appeared to be ecological equivalents based upon external morphology, size, microhabitat preference, and other characteristics, but *Neotoma* is very poor at conserving water (MacMillen, 1964) relative to *T. apereoides*. Individual *T. apereoides* that survived total deprivation were given access to water for 12 hrs in order to roughly simulate a natural situation in which, after a rainless

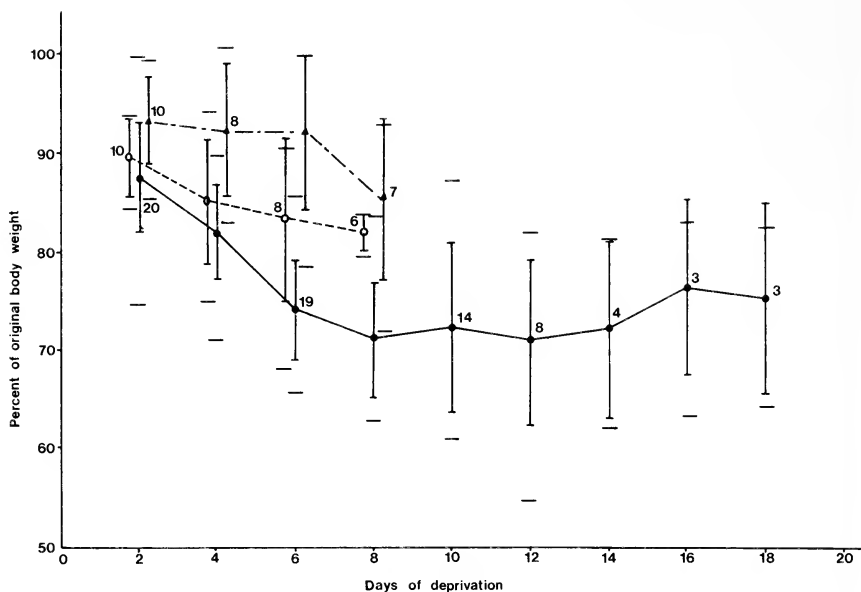


Fig. 2.—Weight response (expressed as percent of initial weight) of *Bolomys lasiurus* during water deprivation experiments. Solid line indicates animals fed corn only, dashed line represents a diet of corn and *Opuntia*, and dot and dash line, a diet of corn and grass. Symbols as in Fig. 1.

interval, a light rain would be collected into small, ephemeral pools in the rocks. The average percent body weight loss incurred during deprivation shrunk from 12.0 to 2.8% (Fig. 1) with only 12 hrs of exposure to free water and probably would have approached or surpassed initial weight had a greater quantity of water been provided.

Laboratory conditions may be more physiologically stressful than natural conditions (Mullen, 1970, 1971a, 1971b). The rocky microhabitats preferred by this echimyid moderate temperature extremes and maintain a higher relative humidity, so weight loss should be reduced even if total deprivation does occur naturally. The collection of rainfall into temporary pools by the rocks is an important advantage which would permit *T. apereoides* to maintain a high level of body weight through occasional access to free water.

In the second deprivation experiment, with *Opuntia* available as an alternate water source, there were again no significant differences in percent weight loss between males and females. By day 8 of the experiment, the mean weight loss of the 14 individuals was 2.5% compared to the 10.0% mean weight loss experienced in the same interval

Table 4.—Mean percent weight loss at death for animals deprived of free water. Arcsine transformed data. Sample size in (). Actual means in [].

Species	Treatments	\bar{x}_1	\bar{x}_2	s_1^2	s_2^2	C	P	
<i>Bolomys lasiurus</i>	corn only, males vs females	33.54 [31.9] (8♂)	35.88 [34.5] (9♀)	10.46	13.76	0.82	>.05	ns
	corn vs corn and <i>Opuntia</i>	34.78 [33.3] (17)	30.80 [26.3] (3)	12.90	8.69	2.05	>.05	ns
<i>Galea spixii</i>	grass only, males vs females	29.60 [24.5] (10♂)	34.00 [31.6] (10♀)	8.56	25.50	2.38	<.05	
	grass vs grass and (♂) <i>Opuntia</i>	29.60 [24.5] (10)	31.60 [27.4] (7)	8.56	3.73	1.70	>.05	ns
	grass vs grass and (♀) <i>Opuntia</i>	34.00 [31.6] (10)	33.30 [30.2] (4)	25.50	2.44	0.40	>.05	ns

by the individuals maintained solely on corn; the difference between the means was very highly significant ($P < .001$; Table 2). Four of the 14 individuals were able to gain weight on this regime. These results confirmed the prediction that *T. apereoides* would be able to utilize *Opuntia* as an alternate water source.

Only one *Thrichomys* died, so no data were collected on the mean number of days until death or the percent original body weight at death. No significant differences existed between sexes on either the corn only diet or the corn and *Opuntia* diet. Overall, mean days survived were the same on both diets (Table 3).

Bolomys lasiurus

No significant difference was found in the comparison of male and female percent body weight change during water deprivation (Table 2). Seventeen of the 20 individuals died during the 18 day experimental period (Fig. 2). This species generally lost weight much more quickly than *T. apereoides*—the 12.2% weight loss after two days without water was approximately the same as the mean (12.0%) loss experienced by *T. apereoides* over 18 days. The individuals of *B. lasiurus* which best maintained body weight still generally lost more weight than the worst cases of weight loss in individual *T. apereoides*. Rapid weight loss during absolute water deprivation was the predicted result. It appears that water stress, coupled with the simultaneous degradation

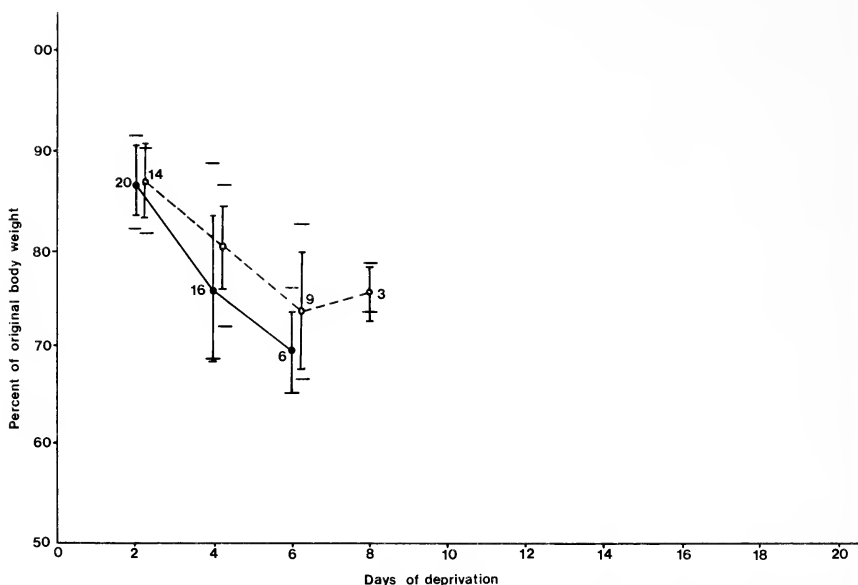


Fig. 3.—Weight response (expressed as percent of initial weight) of *Galea spixii* during water deprivation experiments. Solid line indicates animals fed grass only, dashed line represents a diet of grass and *Opuntia*. Symbols as in Fig. 1.

of habitat quality (cover and water content) during periods of extreme drought may be two causal factors in the boom-bust population fluctuations characteristic of *B. lasiurus* in the Caatinga.

Two groups of *B. lasiurus* were used in the alternate water source experiment. One group received *Opuntia* and the other was given freshly cut grass. Because *Opuntia* is rarely available in the microhabitats occupied by this rodent, it was expected that the secondary compounds might make the cactus unpalatable or prove to be toxic when ingested. On the other hand, grass is generally available in prime *B. lasiurus* microhabitats. Both grass and *Opuntia* functioned to significantly reduce mean percent body weight loss ($.01 < P < .001$ and $P < .001$, respectively; Table 2). However, none of the individuals supplemented with grass died during the 8-day experimental period, while three of 10 supplemented with *Opuntia* and three of 20 given only corn died during the same interval (Fig. 2).

The *B. lasiurus* subjected to total water deprivation lived an average of 10.8 days out of a possible 18 days; no significant difference was found between males and females (Table 3). Comparisons of *B. lasiurus* maintained on the corn only diet with the two groups given alternate water sources did not yield significant results (Table 3).

Table 5.—Mean days to death for animals deprived of free water. Sample size in ().

Species	Treatments	\bar{x}_1	\bar{x}_2	s_1^2	s_2^2	C	P	
<i>Galea spixii</i>	grass only, males vs females	4.30 (10♂)	5.30 (10♀)	1.34	3.34	1.46	>.05	ns
	grass and <i>Opuntia</i> , males vs females	5.60 (7♂)	5.20 (4♀)	0.29	0.92	0.77	>.05	ns
	grass vs grass and <i>Opuntia</i> ,	4.80 (20)	5.45 (11)	2.48	0.48	1.58	>.05	ns
<i>Bolomys lasiurus</i>	corn only, males vs females	9.90 (8♂)	10.00 (9♀)	24.70	1.76	0.06	>.05	ns

Males and females did not differ in mean days until death while on the corn only diet and no difference was found between the group on corn and the group given corn and *Opuntia* (Table 4). Based on a sample size of 17, the mean percent loss of body weight at death was 33.3% for the group subsisting on corn and 26.3% ($N = 3$) for the group maintained on corn and *Opuntia* (Table 4). This difference was not significant ($P > .05$).

The preferred microhabitats of *B. lasiurus*, the early stages of old field succession (Streilein, 1982c), are relatively short-lived and are also subject to severe degradation during dry periods. As cover decreases with increasing aridity, ambient conditions at ground level intensify and predator escape tactics (burrowing through litter or low growing vegetation) cannot function as effectively. All of the advantages inherent in the rocky areas are lacking in the old fields and alternate water sources (for example, cacti) are not available or are subject to lowered water content (for example, grasses). Because *B. lasiurus* does not withstand water deprivation very well, but occupies microhabitats likely to experience severe water stress, this species should be particularly sensitive to the fluctuating environment.

Galea spixii

The high rate of mortality during the absolute water deprivation experiment precluded meaningful statistical comparisons over time. By day 6 of deprivation, two-thirds of the individuals had died and only two of 20 were alive on day 8 (Fig. 3). Individuals typically lost more than 5% of their initial body weight per day.

In the second experiment, the availability of *Opuntia* served to somewhat reduce the average daily percent weight loss, but mortality was still extremely high. *Galea spixii* readily accepted the *Opuntia* pads throughout the experiment, so palatability did not appear to be a factor in the high rate of mortality. *Bolomys lasiurus* and *Thrichomys*

Table 6.—Interspecific comparison of mean percent change in initial body weight for animals deprived of free water. Arcsine transformed data. Sample size in (). Actual means in [].

Species	Treatments	\bar{x}_1	\bar{x}_2	s_1^2	s_2^2	C	P
<i>Thrichomys apereoides</i>	corn only	18.17 [10.0] (20)	32.14 [17.7] (17)	12.61	14.05	11.54	<.001
vs							
<i>Bolomys lasiurus</i>	corn and <i>Opuntia</i>	6.11 [2.5] (14)	24.84 [2.8] (6)	74.09	1.30	7.97	<.001

apereoides generally ate only the cactus pulp, while *G. spixii* typically ate the entire pad, apparently including the trichomes which, considering the quantity eaten, could possibly have had adverse effects.

Galea spixii subjected to complete water deprivation lived an average of 4.8 days, while those given grass and *Opuntia* survived an average of 6.0 days (Table 3). There were no detectable sexual differences in either experiment. Although *Opuntia* did not prevent mortality in the second experiment, the increase in number of days survived did prove to be statistically significant ($P < .05$). Three of 14 individuals given *Opuntia* were still alive after the eighth day; none of the individuals maintained on grass survived that long (Fig. 3). Perhaps *Opuntia* serves only as a temporary, stopgap water source or may be consumed in more moderate quantities with other items in the field. Mares (1975) has suggested that the murid rodent, *Eligmodontia typus*, uses the cactus *Trichocereus candicans* in this manner in the Monte Desert.

Male and female *G. spixii* maintained solely on grass differed significantly ($P < .05$) with respect to mean percent of initial weight at death (Table 4). The average weight of females used in the experiment was 357 g, which was substantially larger than the 310 g average for males. Accordingly, males weighed 75.5% of their initial weight at death and females averaged 68.4% of their initial weight. No statistical differences were found for percent change from initial body weight at death between the grass only and grass and *Opuntia* treatments for males or females (Table 4).

No sex-related differences were found in either the grass only or the grass and *Opuntia* treatment groups with respect to the mean number of days until death. Individuals maintained on grass died, on the average, 5.6 days after the initiation of the experiment, whereas those given grass and *Opuntia* succumbed after an average of 5.2 days (Table 5).

Table 7.—*Interspecific comparisons of mean number of days survived by animals deprived of free water. Sample size in ().*

Species	\bar{x}_1	\bar{x}_2	s_1^2	s_2^2	C	P
<i>T. apereoides</i> vs <i>G. spixii</i>	17.9 (20)	4.8 (20)	0.20	2.48	35.80	$\leq .001$
<i>T. apereoides</i> vs <i>B. lasiurus</i>	17.9 (20)	10.8 (19)	0.20	16.84	7.50	$< .001$
<i>B. lasiurus</i> vs <i>G. spixii</i>	10.8 (19)	4.8 (20)	16.84	2.48	5.97	$< .001$

Interspecific Comparisons

On day 8 of total water deprivation, comparison of mean percent body weight loss between *T. apereoides* and *B. lasiurus* revealed a very highly significant difference ($P < .001$; Table 6). *Thrichomys apereoides* lost on the average only 10.0% of its initial body weight and had no mortality, while *B. lasiurus* lost an average of 28.5% and suffered 15% mortality in the same time interval. *Galea spixii*, on the other hand, had 90% mortality (18 of 20) in the same period. Both *B. lasiurus* and *T. apereoides* lost weight differentially during the corn only and corn and *Opuntia* treatment phases ($P < .001$ in both instances; Table 2). *Thrichomys apereoides*, however, lost only 2.5% of their initial body weight on the average while *Bolomys* lost 17.7%; these means were very highly significantly different ($P < .001$; Table 6). Of the two species, then, *T. apereoides* appears to be better able to withstand total water deprivation and to more efficiently utilize *Opuntia* as an alternate water source. *Galea spixii* performed very poorly in both the water deprivation and alternate water source experiments relative to the performance of *T. apereoides*.

The mean number of days survived by each species is another indication of the relative ability to withstand water deprivation. Out of a possible maximum of 18 days per species, *T. apereoides* survived 17.9 days ($n = 20$) and *B. lasiurus* survived 10.8 days ($n = 19$) on the average. These means are statistically different at the .001 level of significance. If the treatment is considered to be only water deprivation, thereby excluding dietary consideration, *T. apereoides* (17.9), *B. lasiurus* (10.8), and *G. spixii* (4.8; $n = 20$) differed considerably in their ability to withstand water deprivation; each possible pairwise comparison produces a difference at the .001 level of significance (Table

7). With this definition of treatment groups, overall survivorship may also be compared with 95% confidence intervals on the percent surviving until the end of the experiment. Of the initial 20 individuals each of *T. apereoides*, *B. lasiurus*, and *G. spixii*, survivorship was 19 (99.87–75.25), 3 (37.93–3.21), and 0 (16.85–0.00), respectively. *Thrichomys apereoides* is thus significantly different ($P < .05$) from the other two species, which are not distinguishable from one another.

The number of deaths per species under each treatment provides additional information on the mean number of days until death and can also be examined on the basis of percentage of original body weight lost at death. Because only one *T. apereoides* died, between species comparisons are precluded, but the low rate of mortality indicates a high degree of resistance. *Galea spixii* died very quickly and *B. lasiurus* had an intermediate mortality rate. The lower limits of percent body weight loss, below which death occurs, were similar for both species and generally ranged between 25 to 35% regardless of sex or treatment group. *Galea spixii* usually reached these limits in one-half the time observed for *B. lasiurus*.

The ability to withstand water deprivation and use *Opuntia* as an alternate water source varies considerably among the three species examined. *Thrichomys apereoides* is the best by every measure taken and *G. spixii* is by far the worst, with *B. lasiurus* in an intermediate position but somewhat closer to *Galea*. Preference for relatively mesic microhabitats is not inversely correlated with the ability to withstand deprivation.

The physiological capabilities of small mammal faunas often reflect the degree of aridity in their respective environments. This assumes an adequate amount of time available for the development of suitable adaptations or a sufficient level of preadaptation and a comparable selection of habitats. Based strictly upon the total mean annual rainfall, the Caatinga is classified as semiarid. Therefore on a relative scale, the fauna of the Caatinga would not be expected to exhibit as high a level of xeric adaptation as that seen in true desert forms. The relative level of adaptation of four Caatinga species, *Thrichomys apereoides*, *Monodelphis domestica*, *Kerodon rupestris*, and *Wiedomys pyrrhorhinos*, using maximal osmotic concentration of urine as the indicator of degree of adaptation, is given in Table 8.

None of the Caatinga species approach the urine concentrating capabilities of highly adapted desert species such as *Notomys alexis*, *Leggadina hermannsburgensis*, and *Jaculus jaculus*. The values reported for the Caatinga species are based upon mean maximal values, thus the absolute maximum for the species would be somewhat higher. *Thrichomys apereoides* (3394 mosmols/l) and *Monodelphis domestica* (3285 mosmols/l) have moderate urine concentrating capabilities but

Table 8.—Maximal urine concentration in milliosmols for various species of small mammals.

Species	Maximal urine values (mosmols/L)	Locality	Source
<i>Notomys alexis</i>	9370	Australia	MacMillen and Lee (1967)
<i>Leggadina hermannsburgensis</i>	8970	Australia	MacMillen and Lee (1967)
<i>Jaculus jaculus</i>	6500	Africa	Schmidt-Nielsen (1964)
<i>Desmodillus auricularis</i>	6102	Africa	Christian (1976)
<i>Eligmodontia typus</i>	5763	Argentina	Mares (1973)
<i>Dipodomys merriami</i>	5540	North America	Schmidt-Nielsen et al. (1948)
<i>Gerbillus gerbillus</i>	5500	Egypt	Schmidt-Nielsen (1964)
<i>Calomys laucha</i>	5183	Argentina	Mares (1973)
<i>Gerbillus paeba</i>	5029	Africa	Christian (1976)
<i>Notomys cervinus</i>	4920	Australia	MacMillen and Lee (1967)
<i>Dipodomys spectabilis</i>	4090	North America	Schmidt-Nielsen et al. (1948)
<i>Liomys irroratus</i>	3954	Mexico	Christian et al. (1978)
<i>Liomys pictus</i>	3750	Mexico	Christian et al. (1978)
<i>Spermophilus leucurus</i>	3900	North America	Schmidt-Nielsen (1964)
<i>Phyllotis darwini</i>	3619	Argentina	Mares (1973)
<i>Thrichomys apereoides</i>	3394	Brazil	D. Christian (personal communication)
<i>Rhabdomys pumilio</i>	3294	Africa	Christian (1976)
<i>Monodelphis domestica</i>	3285	Brazil	D. Christian (personal communication)
<i>Rattus norvegicus</i> (alb.)	3250		Schmidt-Nielsen et al. (1948)
<i>Peromyscus polionotus</i>	3240	North America	Blackwell and Pivorun (1979)
<i>Peromyscus maniculatus</i>	3239	North America	Blackwell and Pivorun (1979)
<i>Peromyscus leucopus</i>	2725	North America	Blackwell and Pivorun (1979)
<i>Neotoma albigula</i>	2670	North America	Schmidt-Nielsen et al. (1948)
<i>Wiedomys pyrrhorhinos</i>	2542	Brazil	D. Christian (personal communication)
<i>Kerodon rupestris</i>	2119	Brazil	D. Christian (personal communication)

Wiedomys pyrrhorhinos (2542 mosmols/l) and especially *Kerodon rupestris* (2119 mosmols/l) have very weakly developed capabilities. Two of the three *Peromyscus* species are substantially better at conserving water through the production of concentrated urine than *W. pyrrhorhinos* and all three species of *Peromyscus* are superior to *K. rupestris*. This is an unexpected result in light of the fact that the habitats occupied by the *Peromyscus* species receive 1.5–2.5 times more rain on an annual basis than the area around Exu (Streilein, 1982a). The two *Liomys* species which occupy predictable, seasonally dry habitats are also much better urine concentrators than any of the four species from the environmentally unpredictable Caatinga.

Returning to the prediction that physiological capabilities should reflect the degree of environmental aridity, it appears that the small mammal fauna of the Caatinga may have not had a sufficient period of time to adapt to the xeric conditions.

The studies of Mares (1973, 1975, 1976, 1977a, 1977b, 1977c, 1977d, 1980) indicated that the murid rodents in the Monte Desert of Argentina have not evolved highly specialized desert species because the timespan of occupancy has been too brief for the development of such adaptations. Mares further suggested that many of the adaptations to aridity could have evolved as responses to xeric habitats encountered along their Andean invasion route. The Caatinga is located far from the Andes and is surrounded by more mesic biomes, so it is unlikely that colonizing species would possess preadaptations for a xeric environment. An inadequate period of time for the development of suitable adaptations may thus account for the low degree of physiological adaptation observed in the murid rodents of the Caatinga.

Caviomorph rodents and marsupials in the Caatinga also lack pronounced physiological capabilities for water conservation, although they have had a longer period of time to adapt (Patterson and Pascual, 1972). These species have compensated for the aridity with a behavioral rather than physiological response. By preferentially utilizing the more mesic rocky habitats, the caviomorphs and marsupials avoid the most severe environmental conditions. The availability of widespread mesic "microrefugia" in the Caatinga has thus promoted the development of habitat specificity; in most other xeric regions, this option is not available and the small mammal faunas have evolved with a greater reliance upon physiological adaptations.

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ARTICLE 7

HOME RANGE AND USE OF SPACE IN *ZYGODONTOMYS* *LASIURUS* (CRICETIDAE, RODENTIA) IN THE CERRADO OF CENTRAL BRAZIL

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ABSTRACT

Space utilization and distribution of free ranging *Zygodontomys lasiurus* (= *Bolomys lasiurus*) was studied on a 1.3 hectare grid in a natural cerrado habitat in Brasília, Brazil, using a live-trapping procedure. There were five separate survey periods. Densities found were 14, 13, 12, 11, and 9 (mean = 11.80 ± 1.92 SD) individuals per hectare. Home range sizes varied from 200 to 2500 m², most of the adult animals occupying an area of 800 m² (N = 24, mean = 884.16 ± 607.24 SD). Animals were uniformly distributed within the area. Home ranges of adult males overlapped with those of adult females more than with other groups. Adult males had more exclusive space when compared to other individuals in the population.

INTRODUCTION

Home range has been defined as "the area in which an animal travels in its normal activity of food gathering, mating, and caring for young" (Burt, 1943). The area occupied by an animal in a population affects population density, competition between individuals, reproductive success, utilization of food and other resources, social organization, relations between species and other aspects of community and population ecology (Dice and Clark, 1953; Ambrose, 1973; Brise and Smith, 1974; Myton, 1974; Hill, 1977; Alho, 1978, 1979a; Madison, 1980;

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Table 1.—Captures and recaptures of *Zygodontomys lasiurus* per 12-day period in five surveys on the 1.3 hectare grid. The log-likelihood technique tests the null hypothesis that the number of captures or recaptures is independent of survey period.

Survey	Period	Capture	Recapture
I	October 1978	18	41
II	December 1978	17	55
III	February 1979	16	55
IV	April 1979	15	58
V	June 1979	12	27
Total		78	236

Captures: ($G = 1.4$; $df = 4$; $0.9 > P > 0.5$).

Expected captures = 15.6.

Recaptures: ($G = 15.84$; $df = 4$; $P < 0.005$).

Expected recaptures = 47.2.

Smith et al., 1980). The presence of one member of the population affects the utilization of space of another by limiting its movements. This means that individuals would use more space, or at least would utilize space differently, if other individuals were not present in the area. Mares et al. (1980, 1982) presented experimental evidence suggesting that population density and home range size are unrelated parameters. Relative exclusiveness of use of space is defined here as an individual's use of locations or quadrats in relation to other individual use of those locations (Alho, 1979b). It is generally assumed that each species occupies a range within the habitat which may influence population size and behavioral interactions. The present paper shows how much exclusive or shared space *Zygodontomys lasiurus* (= *Bolomys lasiurus*) individuals exhibit within their cerrado habitat.

METHODS

The methods used in this study have been reported in detail elsewhere (Alho, 1979c). The technique employed a moving transect in order to combine the best aspects of single lines of traps and a standard 1.3 ha grid of traps. Moving transects within a grid would minimize the possibility of an animal learning the positions of the traps. The procedure also provides better figures for home ranges, because the recaptures of a given individual represent its movement pattern without the influence of fixed trap sites. The area of the grid was 115×115 m ($13,225$ m²) with 576 capture stations 5 m apart. Two moving transects of 24 traps per line, or 48 traps, were moved daily, during 12 consecutive days of survey for each period of capture. Peanut butter and banana were used as bait. Traps were set at dusk to prevent disturbance by diurnal animals. Five surveys were taken from October 1978 to June 1979, at regular intervals of 7 weeks. Home range sizes were calculated by the minimum area method (Stickel, 1954). The center of activity of the individual was calculated according to the methods proposed by Hayne (1949), Dice and Clark (1953), Jorgensen and Tanner (1963), and Jorgensen (1968). Relative exclusiveness of use of space was done according to Alho (1979b). The study was conducted at the Biological Station of the Universidade de Brasília, Brasília, Brazil. The vegetation for-

Table 2.—*Distribution of the center of activities according to the nearest neighbor method (Clarke-Evans model, 1954, 1955).*

Survey	Density (number per m ²)	Calculated average distance (in m ²)	Expected average distance (in m)	Ratio between expected and calculated	Significance
I	0.00194	21.37	11.35	1.88	$P < 0.01$
II	0.00250	19.65	10.00	1.96	$P < 0.01$
III	0.00138	27.56	13.46	2.05	$P < 0.01$
IV	0.00194	23.37	11.34	2.06	$P < 0.01$
V	0.00197	21.44	11.25	1.90	$P < 0.01$

mation is cerrado, which is a savanna type of vegetation consisting of tall grass and semideciduous xeromorphic trees with a unique appearance of thick bark and twisted trunks. Details on the vegetation and habitat description can be found in Ferri (1977) and Alho (1980).

RESULTS

The number of captures and recaptures of *Z. lasiurus* in the habitat during five different surveys is given in Table 1. To investigate whether the population changed in abundance and activity between periods of surveys, we performed a log likelihood G test (Sokal and Rohlf, 1969), to check whether captures and recaptures were varying significantly from month to month. The analysis showed no significant changes in captures accepting the null hypothesis that all five periods of captures were similar ($G = 1.4$; $df = 4$; $0.9 > P > 0.05$). Recapture is the number of times that previously marked animals were caught by the end of each 12-day period in a grid with moving transects, therefore giving a measure of the movement of individuals in the population. The analysis showed a significant difference of recaptures between periods ($G = 15.84$; $df = 4$; $P > 0.005$).

Table 3.—*Frequencies of home range sizes for individuals with 2 or more recaptures in a 12-day period.*

Home range sizes (in m ²)	Survey periods					Total
	I	II	III	IV	V	
0-300	10	1	6	4	3	24
300-600	2	2	4	2	3	13
>600	3	10	4	7	3	27
Total	15	13	14	13	9	64

$G = 15.88$; $df = 8$; $P < 0.05$. Home range size classes and period of survey are not independent.

Table 4.—*Mean home range sizes (in m²) of individuals with 3 or more recaptures. N = 30.*

Sex and age	Survey periods					Overall mean
	I	II	III	IV	V	
Adult male	675.9	750.4	1875	692.1	846.2	967.9
Adult female	468.2	692.5	1258.2	512.5	466.6	619.6
Young	199.6	301.8	1063.9	307.2	212.5	417.0

The movement of a given animal recorded by the mark-release technique is an array of positions which are the "activity loci." At any given moment a geometric center may be calculated. This center is the so called "center of activity" of that particular individual (Hayne, 1949; Dice and Clark, 1953; Jorgensen and Tanner, 1963). After having all centers of activities calculated for all individuals' home ranges we applied the Clark-Evans model of spatial distribution (Clark and Evans, 1954, 1955), to study the distribution of the centers of activities in our grid (Table 2). The mean distance between a given center of activity chosen at random and its nearest neighbor is tested for deviations from randomness. If the dispersion pattern of the center of activities is at random, the ratio of the expected and observed average distance will be 1. When aggregated, the value of the ratio will be between 0 and 1. The more aggregated the distribution, the closer to 0 will be the ratio. When the distribution is regular, the value of the ratio will be between 1 and 2.1946 (Clark and Evans, 1954, 1955). In all five survey periods we found a regular distribution of the centers of activities.

Home range sizes.—Table 3 shows the frequency of home range sizes by survey period. There is a great variation in home range sizes when number of recaptures ranges from two to 10, but the slope of a regression line is not statistically different from 0. Home range sizes

Table 5.—*Relative exclusiveness of use of space in quadrats of 900 m² in different survey periods according to Alho Model (Alho, 1979). Value represents the percentage of quadrats occupied by a category of individuals compared to all individuals in the population. The larger the value the more exclusive the use of space.*

Survey period	Adult males × other individuals	Adult females × other individuals	Young × other individuals
I	57%	25%	0%
II	65%	25%	22%
III	67%	0%	13%
IV	53%	0%	27%
V	73%	35%	0%

for recaptures over two tend to reach an asymptote with 8 or 10 recaptures. The largest home range in the study area was 2500 m² or less than 20% of the grid. Most of the home ranges were larger than 600 m². We found a significant difference of home range size classes between survey periods ($G = 15.88$; $df = 8$; $P < 0.05$). The adult males had larger home ranges (Table 4).

Relative exclusiveness of use of space.—It is generally assumed that each species occupies a range within the environmental gradient which may influence population size and behavioral interactions. It is important to know how much exclusive or shared space individuals are using in different periods of time. Table 5 summarizes the results of the relative exclusiveness of use of space (Alho, 1979b) by individuals in surveys I through V. Adult males have more exclusive space overlapping fewer home ranges when compared to other members of the population. Usually more than 50% of the grid is exclusively used by the adult male population. Adult females shared more space with other individuals while young had more overlapping home ranges.

DISCUSSION

The densities found during the five survey periods were constant but the movement of the population varied significantly. Home range size classes varied during the period of time studied. During the periods of greatest densities and more movement individuals do not have smaller ranges but overlap somewhat more, and the population occupies more of the available space. The habitat is homogeneous in structure and the distribution of the center of activities is uniform rather than aggregated. Higher densities and movements are thus accommodated by more complete filling of available space and by deeper stacking, rather than by tighter packing of individual's ranges. Adult males have larger home ranges and more exclusive space than adult females and young.

Our surveys suggest that the population was at equilibrium density between October and June, which covers most of the rainy season in the cerrado habitat.

Further work is necessary to determine whether seasonal changes can influence behavioral interactions as a critical proximate factor for abundance and movement of wild cerrado rodents.

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ARTICLE 8

BATS OF THE CENTRAL AFRICAN REPUBLIC (MAMMALIA: CHIROPTERA)

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ABSTRACT

The bats of the Central African Republic are reviewed. The occurrence of 45 species is documented, with locality, habitat, reproductive data, and other natural history information given. Taxonomic notes are discussed where necessary and selected measurements are listed for the species. Twenty species are reported for the first time for the Central African Republic.

INTRODUCTION

Little information is available concerning the bat fauna of the Central African Republic. Most early explorations missed this part of Africa, although Pousargues (1897) reported on his travels in the region between the Ubangui and Shari rivers. Jentink (1885, 1887, 1888) and Matschie (1899) included in their catalogues some specimens from the Central African Republic that were deposited in various European museums. Schwarz (1920) mentioned a small number of bats originating from the vicinity of the Ubangui River in his report of the mammals of Central Africa, but many of his localities were in Zaire. Malbrant (1952) published a report on the mammals and birds of French Central Africa, including the area now in the Central African Republic, but this book was concerned primarily with large mammals and birds. Lucien Blancou spent a number of

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years as a wildlife biologist in the area and published a number of papers containing information on bats (Blancou, 1933, 1935, 1936, 1958). Since then, few reports other than occasional references to bats in various publications have dealt with bats from the Central African Republic.

Two significant collections of bats have been made recently in the Central African Republic. Many of these specimens belong to poorly known taxa or represent species not previously reported from the country and thus help fill gaps in the geographic distributions of these species. This paper constitutes a report on these specimens and reviews previously reported records of bats from the country.

MATERIALS AND METHODS

Robbins spent five nights collecting at three localities in the southern part of the country between 1 December and 31 December 1974. During this interval, 36 specimens representing 12 species were captured. From April 1977 to August 1979, Buchanan served with the U.S. Peace Corps in the Central African Republic and was assigned to the Manovo-Gounda-St. Floris National Park in the northern part of the country. While helping conduct an ecological survey of the Park, a partial inventory of bats was also made. During the inventory, 159 specimens representing 20 species were collected. In addition, unreported specimens of bats from the collections of the Academy of Natural Sciences, Philadelphia, and the American Museum of Natural History, New York, are included in this report.

All cranial and forearm measurements were taken by means of dial calipers and are given in millimeters. Weights are in grams and external measurements are those conventional ones taken by the preparator in the field. All the specimens are deposited in the Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, except those that are reported from the mammal collections of the Academy of Natural Sciences, Philadelphia (ANSP) and the American Museum of Natural History (AMNH). All specimens collected by Robbins are conventional museum study skins; all those collected by Buchanan were initially preserved in formalin but several have subsequently had their skulls removed for identification and study purposes.

Species accounts are arranged in phylogenetic order by families and alphabetical order by genus and species within each family. Remarks on geographic distribution, taxonomy, and natural history are given. Selected measurements are included for all species.

COLLECTING LOCALITIES

In the south, bats were mist netted at three localities:

1. M'Baiki (3°54'N, 18°0'E). This town is within the forest area of southwestern Central African Republic. One mist net was set adjacent to a house on the edge of town; the house was located in groves of mango, papaya, and small cultivated plots. Bats were observed flying around the house before the net was set up. *Micropteropus pusillus*, *Eptesicus tenuipinnis*, *Pipistrellus nanus*, and *Tadarida nigeriae* were caught on 10 and 12 December.

2. 10 km N M'Baiki (4°0'N, 18°0'E). Two nets were placed across a stream in secondary forest adjacent to open cultivated areas on the road to Bangui. One net was placed under the canopy covering the stream; a single *Myotis bocagei* was captured in it. The second net was placed across a small pool (8 meters in diameter) where the stream flowed under the road. The area had scant vegetation with a small

village nearby. The following bats were caught on 11 December: *Hipposideros ruber*, *Mimetillus moloneyi*, *Tadarida leonis*, *T. spurrelli*, and *T. thersites*.

3. Bangassou (4°48'N, 22°46'E). This locality is within the Guinea savanna along the M'bomou River of southeastern Central African Republic. Two nets were set in the town—one along the edge of a house which caught *Scotophilus dinganii*, *Tadarida nigeriae*, and *Micropteropus pusillus*; the other was placed in an open compound adjacent to the house and *Epomophorus gambianus* and *Micropteropus pusillus* were taken. The nets were stationed during the nights of 27 and 28 December.

In the north, eight localities in N'dele Prefecture were sampled for bats. With the exception of location 7, all were within the boundaries of the Manovo-Gounda-St. Floris National Park.

Locations 4, 5, 6, 10, and 12 are within the Sudano-Guinean vegetational zone and occurred in a flat area dominated mostly by *Terminalia laxiflora* vegetation types. Other dominant tree species included *Detarium microcarpum*, *Piliostigma thonningi*, and *Combretum* spp. Degraded termite mounds supporting a closed canopy of dry forest species including *Tamarindus indica*, *Dyospyros mespiliformes*, *Anogeissus leiocarpus*, and *Ficus* spp. are a common feature of the area.

Locations 8, 9, and 11 are situated in the southern portion of the park in the headwaters region of the rivers that irrigate much of the northern plains. The general area is higher in elevation (by as much as 180 meters in places) than the northern locations and consists of a hilly zone of large, weathered rock formations, often sparsely wooded but with lush gallery forest along the water courses. Dominant vegetation in the area includes *Isobерlinia doka*, *Azelia africana*, and *Burkea africana*, with an understory of *Monotes kerstingii* and *Combretum* spp. Trees commonly found in riparian habitats include *Erythrophleum guineense*, *Uapaca samon*, *Vitex* sp., and *Ficus* spp.

4. Gounda Camp, 420 m (9°19'N, 21°12'E). The camp is located in a *Terminalia laxiflora* dominated wooded savanna bordering the Gounda River plain. *Eptesicus somalicus* and *Micropteropus pusillus* were caught in a mist net placed in a grove of *Irvingia smithii* and *Syzygium guineense* next to the river between 10 and 23 June 1978. *S. guineense* was in fruit during this period and fruit bats roosted in this and other similar groves. On 18 and 19 June 1978, 13 individuals from several colonies of *Nycteris hispida* were captured with a hand net in several buildings of the Gounda Camp.

The rainy season was at its peak from 8 to 10 October 1978 and flood waters covered part of the camp. During this period, two *Eptesicus guineensis* and one *E. somalicus* were captured in a mist net placed at the high water mark next to the dining hut. On 13 and 14

October, the net was moved to the top of a large termite mound behind the dining hut where *Eptesicus somalicus*, *Pipistrellus rusticus*, *Sco-toecus hirundo*, and *Hipposideros commersoni* were caught.

5. 1 km N Gounda River crossing at Gounda Camp, 420 m (9°19'N, 21°13'E). This site consisted of a grove of primarily *Syzygium guineense* and was located on the north side of the Gounda River plain opposite Gounda Camp. *Lavia frons* and an unidentified fruit bat were observed roosting in the grove during the day. A mist net was placed within the grove from 19 to 23 June 1978; three *Lavia* were captured in the net.

6. 1½ km NW Koumbala Camp, Koumbala River, 585 m (8°30'N, 20°36'E). Using a sweep net, a single *Nycteris thebaica* was caught from a group of about 40 individuals. These bats were in one of a group of several small caves in a bare limestone area next to the Koumbala River and downstream from Koumbala Camp.

7. Sultan Senoussi, 1 km N N'dele (8°32'N, 20°36'E). This locality is a large cave located high above the present town of N'dele at the site of the stronghold formerly used by Sultan Senoussi early in this century. The cave, with three entrances, consists of a series of crevices, rooms, and passageways. On 26 June 1978, a mist net was draped across the largest opening and additional attempts were made to capture bats with a sweep net as they left via a second entrance during the evening. Several hundred bats of at least four species occupied the cave. *Hipposideros abae*, *Coleura afra*, *Rhinolophus fumigatus*, and *R. landeri* were captured by both hand and mist netting.

8. Matakil Falls, 15 km NW Koumbala Camp, 550 m (8°34'N, 21°10'E). The Koumbala River drops over a large east-west fault at this place, forming a 70–80 meter waterfall from a north-facing precipitous cliff. Adjacent to the falls is a lush gallery forest with tall trees of *Ficus* and other genera bordering the river. Many crevices in rock piles are used as roosting sites for several species of bats. On 25 June 1978, two *Hipposideros ruber* were caught with a sweep net as the bats flew at dusk. On 27 September 1978, a mist net hung inside a narrow rock crevice on the west side of the falls caught four *Taphozous perforatus* from a group of about 12 roosting there. Several other bats of at least two other species were seen hanging from leaning rock slabs but were not captured.

9. Koumbala Camp, 600 m (7°29'N, 21°13'E). This park camp is located on the bank of the Koumbala River where the river flows through an area of bare ironstone shield with interrupted strips of bordering gallery forest. On 2 October 1978, a single *Pipistrellus nanus* was captured in a mist net placed across a bare patch of ironstone along the river adjacent to the dining building.

During the nights of 24 and 25 October 1978, a mist net was set

behind the guest houses 200 meters north of the river. Large *Isoberlina doka* and *Afzelia africana* were present as well as a line of tall *Gmelia arborea* (an introduced exotic) and other small trees of the genera *Burkea*, *Vitex*, and *Prosopis*. Bats of the genera *Scotophilus*, *Eptesicus*, *Epomophorus*, and *Micropteropus* were netted. The flowering and fruiting *I. doka* trees were being visited by numerous fruit bats.

A *Rhinolophus fumigatus* was caught in a hut located next to the river on 21 June 1979 and an *Eptesicus somalicus* was taken in the camp kitchen on 24 June 1979.

Epomophorus gambianus, *Micropteropus pusillus*, *Eptesicus somalicus*, and *Scotophilus nigrnellus* were caught in a mist net set in a garden next to a hut adjacent to the river during the nights of 28 and 29 June 1979. The lush riparian vegetation in the area served as a roosting site for the *Epomophorus* and *Micropteropus*.

10. Gounda River bridge, on National Highway between N'dele and Vakaga, 445 m (8°41'N, 21°30'E). This site is a game guard camp constructed where the main truck route between N'dele and Vakaga crosses the Gounda River. The area, a part of the *Terminalia laxiflora* vegetational zone, is near the edge of where the southern hill country flattens out to the northern plains. A mist net was placed on the bridge over the river on 21 October 1978. Several small bats were observed flying, and a single *Pipistrellus nanus* was caught.

11. Goumba-Koumbala Confluence, 3 km NW Koumbala Camp, 565 m (8°31'N, 21°12'E). This site is an area of large weathered rock formations containing many caves and fissures. Vegetation is largely gallery forest along the rivers and between rock formations but with bare rock predominating. On 26 October 1978 a mist net was set inside a 10 by 20 meter cave containing a colony of about 100 *Coleura afra*, of which 16 were captured.

A large cave consisting of two rooms connected by a narrow passage near the entrance was found next to the Koumbala River, 100 meters up the river from the Goumba confluence. A colony of about 100 *Hipposideros* occupied the back of the cave and a small group of *Rousettus* were hanging near the entrance. A mist net was set in the passageway on 30 June 1979; *R. angolensis* and *H. ruber* were caught. Two other mist nets were set the same night on top of a large rock formation. One net was placed above a crevice containing a colony of bats and the other in an open flyway. One each of *Coleura afra*, *Epomophorus* sp., *Micropteropus pusillus*, and *Rousettus angolensis* were captured.

12. Kaga Doli, 36 km S, 12 km E Gounda Camp, 430 m (9°0'N, 21°17'E). Kaga Doli is an unusual rock formation located in the *Terminalia laxiflora* savanna about 40 km SE Gounda Camp. This large, round-topped rock measuring 90 by 70 meters by 30 meters high is found in an otherwise flat area with little relief for many kilometers in

any direction. The rock is surrounded by a fringe of vegetation consisting of *Anogeissus leiocarpus* dry forest which gives way to the *Terminalia laxiflora* scrub type. Also present is *Hymnocardia acida*, *Crossopteryx febrifuga*, *Piliostigma thonningii*, and *Detarium microcarpum*.

Three mist nets were placed on the east side of the rock near some large crevices containing colonies of *Hipposideros*. On 28 May 1979, 23 *Hipposideros ruber* and eight *H. beatus* were captured in these nets.

ACCOUNTS OF SPECIES

Family Pteropodidae

Epomophorus gambianus (Ogilby, 1835)

1835. *Pteropus gambianus* Ogilby, Proc. Zool. Soc. London, p. 100. Gambia.

Specimens examined (5).—Bangassou, 1 (1♀); Manovo-Gounda-St. Floris National Park, Koumbala Camp, 600 m, 4 (2♂♂, 2♀♀).

Remarks.—*Epomophorus gambianus* is widespread in the Central African Republic. The species has been reported by Jentink (1885:35) from Zemio; Pousargues (1897:253) from the Grande Brousse, located between Yabanda and Mpoko at 7°0'N, 17°50'E; Schwarz (1920:1053) from Fort Crampel and Badingua; and Blancou (1958:10) from N'dele. The material reported by Jentink (1835) was referred to *E. zenkeri* by Matschie (1899:47) and later specimen "b" was referred to *E. wahlbergi* by K. Andersen (1912:523, 525). See account of *E. wahlbergi* under Previously Recorded Species.

The Bangassou female weighed 86 grams when captured on 27 December 1974.

Measurements.—A young adult female from Bangassou: length of forearm, 82.3; condylobasal length, 47.0; alveolar length of maxillary toothrow (C-M²), 15.8.

Micropteropus pusillus (Peters, 1868)

1868. *Epomophorus pusillus* Peters, Monatsber. K. Preussischen Akad. Wiss. Berlin, p. 870. (Gambia, restricted by Andersen, 1912:558–559).

Specimens examined (19).—Bangassou, 4 (2♂♂, 2♀♀); M'Baiki, 4 (2♂♂, 2♀♀); Batangafo, 1 (1♂) (ANSP); Manovo-Gounda-St. Floris National Park, Gounda Camp, 420 m, 1 (1♀); Manovo-Gounda-St. Floris National Park, Koumbala Camp, 600 m, 8 (2♂♂, 6♀♀); Bozoum, 1 (1?) (AMNH).

Remarks.—*Micropteropus pusillus* has been reported from the Central African Republic on two occasions—Pousargues (1897:256) reported an adult female from the Mission Post of the Kemo River, and Blancou (1958:10) listed the species from Zemio. The specimen ex-

amed from Bozoum was collected by L. Blancou on 10 January 1933. The various specimens reported indicate the occurrence of the species from both north and south within the country and it should be expected to occur throughout.

Two females collected on 25 October 1978 at Koumbala Camp were subadults; the remainder were adults. A subadult male was taken on 12 December 1934 at Batangafo and one female captured on 12 December 1974 at M'Baiki was a subadult.

Measurements.—An adult female from M'Baiki: length of forearm, 51.7; condylobasal length, 27.5; alveolar length of maxillary toothrow (C-M²), 8.3.

Rousettus angolensis (Bocage, 1898)

1898. *Cynonycteris angolensis* Bocage, J. Sci. Math., Phys. e Nat., Lisboa, (2)5:133, 138. Pungo Adongo, Angola (9°40'S, 15°40'E, 1220 m—Koopman, 1975:361).

Specimens examined (4)—Manovo-Gounda-St. Floris National Park, Goumba-Koumbala Confluence, 3 km NW Koumbala Camp, 565 m, 4 (2♂♂, 2♀♀).

Remarks.—The four specimens of *Rousettus angolensis* were mist netted in a cave and constitute the first record of the species for the Central African Republic. This species is known from Cameroon (Hayman and Hill, 1971:12) and southern Sudan (Koopman, 1975:361). The presence of the colony in northern Central African Republic would indicate that *R. angolensis* is more widespread and occurs farther north in this region than was formerly thought. These specimens would probably best be referable to the nominate subspecies based on their slightly smaller size than to the more eastern *R. a. ruwenzorii*.

Two of the four specimens captured were subadults on 30 June 1979.

Measurements.—An adult male and female, respectively: length of forearm, 74.4, 75.1.

Family Emballonuridae

Coleura afra (Peters, 1852)

1852. *Emballonura afra* Peters, Reise nach Mossambique, Säugethiere, p. 51. pl. 12; pl. 13, f. 18, 19. Tete Mozambique.

Specimens examined (29).—Sultan Senoussi, 1 km N N'dele, 12 (9♂♂, 3♀♀); Manovo-Gounda-St. Floris National Park, Goumba-Koumbala Confluence, 3 km NW Koumbala Camp, 565 m, 17 (10♂♂, 7♀♀).

Remarks.—*Coleura afra* has been reported previously from two localities in the Central African Republic. Thomas (1915:579) reported the species from Ubangui while Schwarz (1920:1048) listed British Museum material from Kaga Djiirri. Kock (1969a:70) gave a more precise location for Kaga Djiirri—25 mi W Fort Sibut, on the Tomi River,

Krebeji (5°44'N, 18°50'E). Based on the present records from the north, and in view of the records listed by Kock (1969a), *Coleura afra* should be found throughout the country.

Measurements.—Two adult males followed by two adult females: length of forearm, 51.9, 50.5, 50.2, 49.3.

Taphozous mauritanus E. Geoffroy, 1818

1818. *Taphozous mauritanus* E. Geoffroy, Description de l'Egypte, 2:127. Mauritius Island.

Specimens examined (3).—Fort Sibut, 3 (2♂♂, 1♀) (ANSP).

Remarks.—*Taphozous mauritanus* was listed by Blancou (1936:41) as occurring in Central African Republic but he gave no specific locality nor reference to specimens. However, one can infer from the text that the locality would be the post of Bozoum and the environs of the upper Ouham, Nana Barya, and Pende river valleys in north-western Central African Republic. Later, Blancou (1958:10) recorded the species from Bozoum and Fort Crampel.

Three specimens in the collection of mammals of the Academy of Natural Science of Philadelphia were taken at Fort Sibut. An adult male was captured on 27 September 1934, whereas an adult female and a juvenile female were obtained on 17 October 1934.

Measurements.—An adult male followed by an adult female: length of forearm, 60.6, 61.8; condylobasal length, 18.9, 19.7; alveolar length of maxillary toothrow (C-M³), 8.4, 8.8.

Taphozous perforatus sudani Thomas, 1915

1915. *Taphozous sudani* Thomas, Ann. Mag. Nat. Hist., ser. 8, 15:561. Mongalla, Sudan.

Specimens examined (4).—Manovo-Gounda-St. Floris National Park, Matakil Falls on Koumbala River, 15 km NW Koumbala Camp, 550 m, 4 (4♂♂).

Remarks.—These specimens are the first records of *Taphozous perforatus* reported for the Central African Republic. Following Koopman (1975), the four adult males are tentatively assigned to *Taphozous perforatus sudani* based on their size. They do not exhibit the gray-brown pelage color of the more western African specimens referable to *T. p. swirae* described from northern Nigeria; instead they are rather dark brown in color.

The weights of the four specimens are 20.4, 20.2, 19.3, and 19.6 grams.

Measurements.—Selected measurements of four adult males: length of hind foot, 13, 13, 14, 12; length of forearm, 61.0, 60.7, 61.4, 62.2.

Family Nycteridae

Nycteris arge Thomas, 1903

1903. *Nycteris arge* Thomas, Ann. Mag. Nat. Hist., ser. 7, 12:633. Efulen, Cameroon.

Specimens examined (2).—Salo, 2 (1♂, 1♀) (AMNH).

Remarks.—These specimens from the southwestern region are the first records of this widespread forest species from the Central African Republic. Judging from its abundance in adjacent countries, *N. arge* should be found throughout the southern parts of the country in suitable habitat.

Measurements.—Selected measurements of a female and a male, respectively: length of ear, 30, 29; length of forearm, 44.0, —.

Nycteris hispida hispida (Schreber, 1775)

1775. *Vespertilio hispidus* Schreber, Säugthiere, 1:169, 188, pl. 56. Senegal.

Specimens examined (16).—Manovo-Gounda-St. Floris National Park, Gounda Camp, 420 m, 13 (6♂♂, 7♀♀); Birao, 2 (2?) (AMNH); Nola, 1 (1?) (AMNH).

Remarks.—*Nycteris hispida* was first reported from the Central African Republic by Blancou (1958:10) with material from N'dele, near the Gounda River. This is probably the material referred to by Malbrant (1952:208) from the Gounda Plain. The specimens reported herein are from the north and south so the species should be found throughout the country as the species is in general widespread in the forest and savanna regions of Africa.

Of the series of 13 specimens taken on 18 and 19 June 1978, only two females were adults; one of these was lactating. The remainder exhibited unfused epiphyses, but were nearly adult in size.

Measurements.—Two adult females: length of ear, 21, 21; and length of forearm, 39.2, 39.1.

Nycteris thebaica labiata Heuglin, 1861

1861. *Nycteris labiata* Heuglin, Nova Acta Acad. Caes. Leop.-Carol., Halle, 29(8):5. Keren, Eritrea, Ethiopia.

Specimen examined (1).—Manovo-Gounda-St. Floris National Park, 1½ km NW Koumbala Camp, Koumbala River, 585 m, 1 (1♀).

Remarks.—A single old adult female was captured on 26 June 1978. This individual is assigned to *Nycteris thebaica labiata* based on its intermediate size. Koopman (1975) regarded central and southern Sudanese specimens as belonging to this taxon, although Kock (1969a) considered all Sudanese specimens as members of the large, northern nominate subspecies. The western Africa subspecies *N. t. gambiensis* is yet smaller than either of the above mentioned ones.

Nycteris thebaica has been reported previously from the Central African Republic by Pousargues (1897:259) from Mission Post on the Kemo River. This species should occur commonly throughout the country.

Measurements.—Length of ear, 32; length of forearm, 45.1.

Family Megadermatidae

Lavia frons affinis Andersen and Wroughton, 1907

1907. *Lavia frons affinis* Andersen and Wroughton, Ann. Mag. Nat. Hist., ser. 7, 19:140. Kaka, Upper Nile Province, Sudan.

Specimens examined (3).—Manovo-Gounda-St. Floris National Park, 1 km N Gounda River crossing at Gounda Camp, 420 m, 3 (2♂♂, 1♀).

Remarks.—*Lavia frons* is a widespread species in the savannas of this part of Africa. In addition to our records from the northern part of the country, the species has been reported by Jentink (1885:35) from Zemio and by Blancou (1958:10) from Aouk near N'dele and Haut-Mbomou near Zemio. Certainly this species is more common and widespread in the country than these few records would suggest.

The weights of the males followed by the single female are, respectively, 18.6, 19.6, and 18.3 grams.

Measurements.—Two adult males followed by an adult female: length of forearm, 58.3, 57.6, 59.4.

Family Rhinolophidae

Rhinolophus fumigatus Rüppell, 1842

1842. *Rhinolophus fumigatus* Rüppell, Museum Senckenburgianum, 3:132, 155. Shoa Province, Ethiopia.

Specimens examined (10).—Manovo-Gounda-St. Floris National Park, Koumbala Camp, 600 m, 1 (1♀); Sultan Senoussi, 1 km N N'dele, 9 (6♂♂, 3♀♀).

Remarks.—These specimens of *Rhinolophus fumigatus*, the first recorded for the Central African Republic, are large for the species in this part of Africa. Koopman (1975:389) regarded *R. f. fumigatus* from Ethiopia as large (forearm 51–53, condylocanine 19.6–20.3), *R. f. exsul* in Sudan as small (forearm 47–49, condylocanine 18.6–19.0), and *R. f. abae* as slightly larger than *R. f. exsul* (forearm 48–53, condylocanine 18.6–19.6). In addition, *R. f. foxi*, originally described from northern Nigeria, appears, based on West African specimens, to be close to the nominate subspecies in size (Aellen, 1952:60 and Rosevear, 1965:211). We are not able to assign our specimens to subspecies although they are close to both *R. f. fumigatus* and *R. f. foxi* in size.

Measurements.—An adult male from Sultan Senoussi and an adult female from Koumbala Camp, respectively: length of forearm, 53.8, 52.4; condylocanine length, 20.7, 20.5; alveolar length of maxillary tooththrow (C-M³), 8.2, 8.3.

Rhinolophus landeri Martin, 1838

1838. *Rhinolophus landeri* Martin, Proc. Zool. Soc. London, for 1837, p. 101. Fernando Po.

Specimens examined (2).—Sultan Senoussi, 1 km N N'dele, 2 (2♀ ♀).

Remarks.—*Rhinolophus landeri* is widespread in sub-Saharan Africa although these two specimens are the first records for the Central African Republic. The two individuals were in the orange-red color phase when captured on 26 June 1978. As in the case of *R. fumigatus*, a study of geographic variation of *R. landeri* is needed. *R. landeri lobatus* and *R. l. dobsoni* have been reported from Sudan (Koopman, 1975:388), whereas *R. l. landeri* is considered by Kock (1969a:117–119) to occur in West Africa as far east as Cameroon. Mensural differences between these taxa appear slight, and we are unable to assign our specimens to subspecies pending a more detailed look at subspecific variation.

Measurements.—Length of forearm 44.7, 42.4.

Family Hipposideridae

Hipposideros abae J. A. Allen, 1917

1917. *Hipposideros abae* J. A. Allen, Bull. American Mus. Nat. Hist., 37:432. Aba, Oriental Province, Zaire.

Specimens examined (9).—Sultan Senoussi, 1 km N N'dele, 6 (1♂, 5♀ ♀); Manovo-Gounda-St. Floris National Park, Goumba-Koumbala Confluence, 3 km NW Koumbala Camp, 565 m, 3 (3♀ ♀).

Remarks.—*Hipposideros abae* is generally confined to the forest block in tropical Africa from the west coast as far east as Sudan (Koopman, 1975) and Uganda (Hill, 1963). The specimens from the Central African Republic, the first records for the country, are from the edge of the Doka woodland zone in the northern region.

The six specimens collected at Sultan Senoussi were captured on 21 June 1978. A single adult gray male was taken; the remainder were females and included two subadults. The pelage of the adult females ranged from an intense red-orange to gray in color.

Measurements.—Two adult females and one adult male from Sultan Senoussi, respectively: length of forearm, 57.5, 61.2, and 58.0.

Hipposideros beatus beatus K. Andersen, 1906

1906. *Hipposideros beatus*, K. Andersen, Ann. Mag. Nat. Hist., ser. 7, 17:279. 15 mi from Benito River, Rio Muni, Equatorial Guinea.

Specimens examined (8).—Manovo-Gounda-St. Floris National Park, Kaga Doli, 36 km S, 12 km E Gounda Camp, 430 m, 8 (5♂ ♂, 3♀ ♀).

Remarks.—Although previously unreported from the Central African Republic, *Hipposideros beatus* has been reported from Sierra

Leone to southwestern Sudan and northeastern Zaire (Hayman and Hill, 1971). Koopman (1975) referred specimens from Sudan and northeastern Zaire to *H. b. maximus* Verschuren, 1957, which was described from Garamba National Park, Zaire. However, the single adult female is essentially identical in size to specimens from southern Cameroon and so all are referred to the nominate subspecies.

The specimens were taken on 29 May 1979. A lactating female was captured; the remaining specimens are subadults, but judging from their size, they were likely no longer nursing.

Measurements.—A single adult female: length of forearm, 44.7, condylocanine length, 13.9; alveolar length of maxillary tooththrow (C-M³), 5.0; crown breadth across last upper molars, 5.5.

Hipposideros commersoni gigas (Wagner, 1845)

1845. *Rhinolophus gigas* Wagner, Arch. f. Naturgesch., 11(1):148. Benguela, Angola.

Specimen examined (1).—Manovo-Gounda-St. Floris National Park, Gounda Camp, 420 m, 1 (1♀).

Remarks.—A single adult female *Hipposideros commersoni* was caught using a mist net placed on top of a large termite mound. This specimen, the first record of the species for the Central African Republic, must certainly come from the extreme northeastern edge of the range of this species in this region of Africa. Generally, *H. commersoni* is widespread and common in the woodland and forest zones to the south.

Measurements.—Length of forearm, 94.0.

Hipposideros ruber centralis K. Andersen, 1906

1906. *Hipposideros caffer centralis* K. Andersen, Ann. Mag. Nat. Hist., ser. 7, 17:275, 277. Entebbe, Uganda.

Specimens examined (27).—Manovo-Gounda-St. Floris National Park, Matakil Falls on Koumbala River, 15 km NW Koumbala Camp, 550 m, 2 (1♂, 1♀); Manovo-Gounda-St. Floris National Park, Kaga Doli, 36 km S, 12 km E Gounda Camp, 430 m, 23 (10♂♂, 13♀♀); Manovo-Gounda-St. Floris National Park, Goumba-Koumbala Confluence, 3 km NW Koumbala Camp, 1 (1♀); 10 km N M'Baiki, 1 (1♂).

Remarks.—Pousargues (1897:258) reported a female from Bangui as *H. caffer*; that specimen was later referred by Schwarz (1920:1048) to *H. caffer ?centralis*. This subspecies is generally now referred to the species *H. ruber* (Hayman and Hill, 1971:29). In addition to the Bangui record, Blancou (1958:10) recorded *Hipposideros (caffer or abae?)* from Bozoum. Unfortunately we are unable to determine the proper identity of either of the reported records; *H. abae*, *H. caffer*, or *H. ruber* could have been taken.

Some of the specimens from Kaga Doli were reproductively active; all seven adult females were lactating. Thirteen juveniles had unfused

epiphyses. The four specimens from the other three localities were adults.

The adult male from 10 km N M'Baiki weighed 11 grams.

Measurements.—Two adult males followed by two adult females from Kaga Doli: length of forearm, 50.3, 51.2, 50.0, 52.2; condylocanine length, 15.6, 16.0, 16.1, 15.9; alveolar length of maxillary tooththrow (C-M³), 6.1, 6.1, 5.9, 5.7.

Family Vespertilionidae

Eptesicus guineensis (Bocage, 1889)

1889. *Vesperus guineensis* Bocage, J. Sci. Math., Phys. e Nat., Lisboa (2) 1:6. Bissau, Guinea Bissau.

Specimens examined (3).—Manovo-Gounda-St. Floris National Park, Gounda Camp, 420 m, 3 (3♀).

Remarks.—The taxonomy of the small, dark-winged species of the genus *Eptesicus* in Africa is in a confused state. *E. guineensis*, the smallest of these species, has been referred to in the past as *E. minutus* and *E. pusillus* (see Koopman, 1975:406–407 for discussion of these names). In the Central African Republic, Blancou (1933:22 and 1935:65–66) referred specimens from the Ouaka and Kankjia river valleys to the species *Vesperus minutus*. Later, Blancou (1958:10) reported *Eptesicus pusillus* from Bozoum. We are unable to identify to species these reported bats.

Three adult females were the only representatives of the small *E. guineensis* of the 21 *Eptesicus* captured in northern Central African Republic. The species seems to be distributed primarily in West Africa, although Koopman (1975:407) reported a record from Kyabe, southern Chad, and documented its occurrence in Sudan and northeast Zaire.

Measurements.—Three adult females: length of forearm, 29.1, 30.4, 28.6; condylobasal length, 10.7, 10.9, –; and alveolar length of maxillary tooththrow (C-M³), 3.6, 3.5, 3.8.

Eptesicus somalicus (Thomas, 1901)

1901. *Vespertilio minutus somalicus* Thomas, Ann. Mag. Nat. Hist., ser. 7, 8:32. Har-gaissa, Somalia.

Specimens examined (18).—Manovo-Gounda-St. Floris National Park, Gounda Camp, 420 m, 11 (5♂♂, 6♀♀); Manovo-Gounda-St. Floris National Park, Koumbala Camp, 600 m, 7 (2♂♂, 5♀♀).

Remarks.—Based on the collection from northern Central African Republic, *Eptesicus somalicus* seems to be relatively more abundant than is *E. guineensis*. Thus, the previously reported records of small *Eptesicus* from the Central African Republic may be referable to this species (see account of *E. guineensis*). Although *E. somalicus* as cur-

rently understood is generally an eastern and southern African species, it has been recently reported from Mbe, Cameroon (Aellen, 1952:85; Rosevear, 1965:258); Pandam, Nigeria (Bergmans, 1977:282); Nobere, Upper Volta (Koopman et al., 1978:4); Atakpame and Temedja, Togo (De Vree et al., 1969:206), and Namoundjoga, Togo (De Vree et al., 1970:45). Vielliard (1974:985) records a single male from Fort-Archambault, Chad. The records from the Manovo-Gounda-St. Floris National Park together with the records from West Africa would indicate the species should be found throughout the Central African Republic.

All of the specimens collected were adults. Only a single female evidenced reproductive activity; it was lactating on 17 June 1978.

Measurements.—Two adult males and two adult females from Gounda Camp, respectively: length of forearm, 29.3, 30.0, 29.9, 31.9; condylobasal length, 11.8, 11.7, 12.3, 11.8; and alveolar length of maxillary tooththrow (C-M³), 4.1, 4.1, 4.3, 4.2.

Eptesicus tenuipinnis tenuipinnis (Peters, 1872)

1872. *Vesperus tenuipinnis* Peters, Monstb. K. Preuss. Akad. Wiss., Berlin, p. 263. Guinea.

Specimens examined (5).—M'Baiki, 5 (3♂♂, 2♀♀).

Remarks.—These bats, all adults, were netted on two separate nights; four on 10 December and a single male on 12 December. Supernumerary upper first premolars are present on both maxillaries of CM 41057, an adult male, thus giving this individual the upper dental formula of *Pipistrellus*.

These specimens are the first of this species recorded from the Central African Republic. It is to be expected only in the forested parts of the southwestern corner of the country, and probably reaches the northern limits of its range in this region.

Three adult males averaged 4.3 g in weight, ranging from 4 to 5; two adult females weighed 4 and 5 g, respectively.

Measurements.—Two adult males followed by two adult females, respectively: length of forearm, 27.5, 29.5, 28.3, 28.9; condylobasal length, 11.5, 11.4, 11.5, 11.3; alveolar length of maxillary tooththrow (C-M³), 4.2, 4.0, 3.9, 3.9.

Mimetillus moloneyi moloneyi (Thomas, 1891)

1891. *Vesperugo (Vesperus) moloneyi* Thomas, Ann. Mag. Nat. Hist., ser. 6, 7:528. Lagos, Nigeria.

Specimen examined (1).—10 km N M'Baiki, 1 (1♀).

Remarks.—A single adult female, weighing 8.0 g, was captured on 11 December 1974, and constitutes the first record of this species for the Central African Republic. It is assigned to the nominate subspecies of western Africa.

Measurements.—Length of forearm, 27.9; condylobasal length, 12.4; alveolar length of maxillary toothrow (C-M³), 4.3.

Myotis bocagei cupreolus Thomas, 1904

1904. *Myotis bocagei cupreolus* Thomas, Ann. Mag. Nat. Hist., ser. 7, 13:407. Efulen, Cameroon.

Specimen examined (1).—10 km N M'Baiki, 1 (1♂).

Remarks.—This specimen is the first correct record of the rufous mouse-eared bat for the country. Previously, Schwarz (1920:1057) reported a single female from Duma in a collection taken along the Ubangui River by Schubotz. Duma is located in Zaire, on the east side of the river. Davis and Misonne (1964) incorrectly listed Duma in Central African Republic, but did give correct coordinates.

Based upon the dark color of the dorsal pelage, this specimen is assigned to the West African forest subspecies *cupreolus*. It has a suggestion of a light, third band between the normal two bands of color on the hairs of the dorsum.

Measurements.—Length of forearm, 35.9; condylobasal length, 13.4; alveolar length of maxillary toothrow (C-M³), 5.2.

Pipistrellus nanus (Peters, 1852)

1852. *Vespertilio nanus* Peters, Naturwissenschaftliche Reise nach Mozambique. Zoologie. 1. Säugethiere. p. 16, pl. 16, fig. 2. Inhambane, Mozambique.

Specimens examined (3).—M'Baiki, 1 (1♀); Manovo-Gounda-St. Floris National Park, Gounda River bridge, on National Highway between N'dele and Vakaga, 445 m, 1 (1♂); Manovo-Gounda-St. Floris National Park, Koumbala Camp, 600 m, 1 (1♂).

Remarks.—*Pipistrellus nanus* was first reported for the Central African Republic from Bangui by Pousargues (1897:262). This species is widespread in sub-Saharan Africa (Hayman and Hill, 1971), and thus is expected in the Central African Republic. The records from the Manovo-Gounda-St. Floris National Park are near the northern limits of the geographic range of *P. nanus*; it is known from Sudan (Kock, 1969a:171); Koopman, 1975:399) and southern Chad (Schwarz, 1920:4057; Zimara, 1935:10).

Measurements.—Adult female from M'Baiki: length of forearm, 28.2; condylobasal length, 11.0; and alveolar length of maxillary toothrow (C-M³), 3.7.

Pipistrellus rusticus marrensis Thomas and Hinton, 1923

1923. *Pipistrellus marrensis* Thomas and Hinton, Proc. Zool. Soc. London, p. 249. Foothills of southern Jebel Marra, Darfur Province, Sudan.

Specimens examined (6).—Manovo-Gounda-St. Floris National Park, Gounda Camp, 420 m, 6 (3♂♂, 3♀♀).

Remarks.—Koopman (1975) reviewed the distribution and taxono-

my of *Pipistrellus rusticus marrensis* in Sudan and also reported a record from western Ethiopia. In reviewing the taxonomic relationship and geographic distribution of the species, Hill (1976) reported specimens of *P. r. marrensis* from Kenya, Cameroon, and Ghana. A large geographic hiatus separates *P. r. marrensis* in Kenya from the northern geographic limits of the nominate subspecies in Zambia. Our specimens are the first recorded from Central African Republic. It is likely that this species is more widespread in West and East Africa than these records imply; perhaps some specimens in collections have been confused with the closely similar *P. kuhlii*.

Two males were netted on 13 October 1978 and one male and three females were captured the following night.

Measurements.—Two adult males followed by two adult females, respectively: length of forearm, 26.6, 27.1, 28.3, 27.8; condylobasal length, 10.3, 10.9, 11.4, 10.7; alveolar length of maxillary tooththrow (C-M³), 3.5, 3.7, 3.8, 3.5.

Scotoecus hirundo (de Winton, 1899)

1899. *Scotophilus hirundo* De Winton, Ann. Mag. Nat. Hist., ser. 7, 4:355. Gambaga, Ghana.

Specimen examined (1).—Manovo-Gounda-St. Floris National Park, Gounda Camp, 420 m, 1 (1♀).

Remarks.—A single young-adult male, captured in a mist net on 14 October 1978, is the first record of this species for the country. It has been reported from northern Cameroon (Hill, 1974), southwestern Chad (Vielliard, 1974), and southern Sudan (Hill, 1974; Kock, 1969a; Koopman, 1975). We follow Robbins (1980) in assigning all dark-winged specimens to the species *S. hirundo*, with *S. hindei* as a synonym, even though there is still some difficulty in allocating all East African specimens to a single size group. We are unable to assign our young-adult to subspecies as defined by Robbins (1980:84). It appears from measurements given by Hill (1974:184–185) and Robbins (1980:84) that western individuals are smaller than eastern ones. Vielliard (1974:987) felt his specimens agreed with the East African subspecies *S. h. hindei* but the measurements given would indicate that his specimen is small for the subspecies. In spite of the young age of our specimen, it seems nearer the nominate subspecies in size, but a definitive allocation of *S. hirundo* from the Central African Republic to subspecies must await the acquisition of additional specimens, especially adults.

Both small, upper premolars are present in the specimen from Central African Republic.

Measurements.—Length of forearm, 31.0; condylobasal length, 11.7; alveolar length of maxillary tooththrow (C-M³), 4.3.

Scotophilus dinganii (A. Smith, 1833)

1833. *Vespertilio dinganii* A. Smith, S. Afr. Quart. J., 2:59. Between Port Natal and Delagoa Bay.

Specimens examined (2).—Bangassou 2 (1♂, 1♀).

Remarks.—These two specimens constitute the first report of this species for the Central African Republic. The taxonomy of the smaller African species of the genus *Scotophilus* is in a confused state (Kock, 1969a; Koopman, 1975; Koopman et al., 1978; Robbins, 1978; Hill, 1980; Robbins, 1980). Our two specimens are assigned to the large species now referred to as *S. dinganii*. They are considerably larger than *S. nigritellus* of West Africa or *S. leucogaster* from the Sudan (as given by Koopman, 1975:415), and seem to be closest in size, as well as in color, to *S. nux*, considered by Hayman and Hill (1971:50) to be a subspecies of *S. nigrita* (= *S. dinganii*).

Measurements.—An adult male followed by an adult female: length of forearm, 51.0, 52.7; condylobasal length, 18.5, 18.5; alveolar length of maxillary tooththrow (C-M³), 6.5, 6.5.

Scotophilus nigritellus de Winton, 1899

1899. *Scotophilus nigritellus* de Winton, Ann. Mag. Nat. Hist., ser. 7, 4:355. Gambaga, Ghana.

Specimens examined (6).—Manovo-Gounda-St. Floris National Park, Koumbala Camp, 600 m, 6 (5♂♂, 1♀).

Remarks.—These six specimens are the first record of *Scotophilus nigritellus* from the Central African Republic. Our specimens seem to agree best in size with the smallest species of *Scotophilus*, *S. nigritellus*, but this allocation is tentative pending a much needed revision of the genus in Africa clarifying the taxonomic relationship of the group of small species (see comments in previous account).

Measurements.—Three adult males: length of forearm 45.4, 45.4, 45.9; condylobasal length, 16.0, 15.9, 16.2; alveolar length of maxillary tooththrow (C-M³), 5.7, 5.4, 5.5.

Family Molossidae

Tadarida leonis (Thomas, 1908)

1908. *Nyctinomus leonis* Thomas, Ann. Mag. Nat. Hist., ser. 8, 2:373. Sierra Leone.

Specimens examined (3).—10 km N M'Baiki, 3 (2♂♂, 1♀).

Remarks.—*Tadarida leonis* is confined to the African forest block, and is numerically common and widely distributed in this zone from extreme West Africa at least as far east as Uganda (Koopman, 1975:420). It probably reaches the northern extreme of its geographic range in the forests of southern Central African Republic where these

specimens were captured. These three specimens are the first records of the species for the country.

Measurements.—Two adult males followed by an adult female, respectively: length of forearm, 40.6, 36.4, 40.2; condylobasal length, 18.6, 17.0, 18.4; alveolar length of maxillary tooththrow (C-M³), 7.0, 6.5, 7.1.

Tadarida nigeriae nigeriae (Thomas, 1913)

1913. *Chaerophon nigeriae* Thomas, Ann. Mag. Nat. Hist., ser. 8, 11:319. Zaria Province, Nigeria.

Specimens examined (6).—Bangassou, 3 (3♂♂); M'Baiki, 3 (3♂♂).

Remarks.—These specimens are the first of this species to be recorded from the Central African Republic. Hayman and Hill (1971:62) regarded all specimens of this species from the northern part of the range as the nominate subspecies based upon the dark wing pigmentation. Our specimens agree with their determination in color of the wings and do not show any of the pale wing color as reported by Koopman (1965:21) for a Niangara, Zaire, specimen. Although specimens of *T. nigeriae* only were obtained in the south, recent records from Ethiopia (Hill and Morris, 1971:47), Chad (Vielliard, 1974:988), and Niger (Kock, 1978:119–121) indicate that the species occurs north of the forest block and should be found throughout the country.

All specimens from both localities were adult males. Weights of six adult males averaged 16.3 and ranged from 15 to 17.

Measurements.—Two adult males from Bangassou: length of forearm, 45.9, 47.1; condylobasal length, 18.4, 18.5; alveolar length of maxillary tooththrow (C-M³), 6.9, 7.0.

Tadarida spurrelli (Dollman, 1911)

1911. *Xiphonycteris spurrelli* Dollman, Ann. Mag. Nat. Hist., ser. 8, 7:211. Bibianaha, 60 mi W Kumasi, Ghana.

Specimens examined (5).—10 km N M'Baiki, 5 (4♂♂, 1♀).

Remarks.—Koopman (1975) considered the genus *Xiphonycteris* Dollman, 1911, to be a valid subgenus of *Tadarida*, although Freeman (1981) placed all species formerly included in *Xiphonycteris* and *Mops* in the latter and recognized it as a separate genus. Mohamed El Rayah (personal communication) has revised the *Xiphonycteris-Mops* complex of species and considers *Mops*, with *Xiphonycteris* as a synonym, as a valid subgenus of *Tadarida*.

Tadarida spurrelli (Dollman, 1911) had been considered a rare species (Rosevear, 1965:350) but recent reports indicate a wider distribution (Kock, 1969b; De Vree, 1969). These five specimens are the first records of this species for the Central African Republic. Undoubt-

edly, this species is more widespread than the few published records would indicate; some specimens may have been confused with *Tadarida nanula*, although *T. spurrelli* can be readily distinguished by its smaller size and dark ventral pelage.

All five of the specimens were adults when captured on 11 December 1974. The single female was smaller than males as had been reported by others.

Measurements.—Two adult males and one adult female, respectively: length of forearm, 28.9, 28.9, 27.2; condylobasal length, 14.3, 14.4, 13.7; alveolar length of maxillary tooththrow (C-M³), 5.8, 5.8, 5.7.

Tadarida thersites (Thomas, 1903)

1903. *Nyctinomus thersites* Thomas, Ann. Mag. Nat. Hist., ser. 7, 12:634. Efulen, Cameroon.

Specimens examined (2).—10 km N M'Baiki 2 (1♂, 1♀).

Remarks.—A forest block species occurring from West to East Africa, *T. thersites* only was taken in the south of the Central African Republic. This locality of record is probably near the northern limits of its range in this part of Africa as it probably does not intrude very far in the Guinea savanna zone. These specimens are the first records for the Central African Republic.

Measurements.—An adult male followed by an adult female: length of forearm, 39.9, 36.4; condylobasal length, 17.5, 16.5; alveolar length of maxillary tooththrow (C-M³), 6.7, 6.5.

PREVIOUSLY RECORDED SPECIES

Hypsignathus monstrosus H. Allen, 1861.—This species was recorded by Pousargues (1897:250) from Bangui. Schwarz (1920:1048) mentioned the same material.

Eidolon helvum (Kerr, 1792).—Matschie (1899:63) listed three males from Semio (=Zemio) in the Berlin Museum. The straw-colored fruit bat has been reported tentatively from the Kankjia and Ouaka river valleys (Blancou, 1933:22, Blancou, 1935:65); Grimari (Blancou, 1935:65); and the post of Bozoum and the environs of the upper valleys of the Ouham, Nana Barya and Pende rivers (Blancou, 1936:41). Blancou (1958:10) recorded the species from Bozoum and Zemio.

Epomophorus anurus Heuglin, 1864.—Schwarz (1920:1053) and Kock (1969a:19) recorded this species from the Middle Shari River. Blancou (1936:41) referred material with a questionable identification from the post of Bozoum and environs of the upper valleys of the Ouham, Nana Barya and Pende rivers to this species. Kock (1969a:18) and Koopman (1975:364) included this species in *E. labiatus*.

Epomophorus pousarguesi Troussart, 1904.—Pousargues (1897:253)

reported this species from "Grande Brousse, between Yobanda and Mpoko (Upper Shari River, *ca.* 7°0'N, 20°15'E)". This locality was corrected by Bergmans (1978:684) to "between Mpoko (near Makorou) and Yobanda" at 6°30'N to 7°30'N, 19°45'E to 20°15'E. Bergmans (1978:682, 686) gave an additional locality at Bangui, Poste de la Mission Haut Kemo, and Blancou (1958:10) listed the species from Bozoum. To our knowledge, these are the only localities from which this species has been reported.

Epomophorus wahlbergi (Sundevall, 1846).—Matschie (1899:42) recorded this species from Semmio [=Zemio]. The same material was reported by Andersen (1912:524). Matschie (1899:47) also referred Jentink's (1885:35, 1887:251, 1888:137) specimen "b" from Semmio to a new species *E. zenkeri*, but Andersen (1912:525) referred all of Matschie's examined material of *E. zenkeri* from the Berlin Museum to *E. wahlbergi*. Based on Andersen's (1912:523) synonymy, this would appear to include specimen "b" as well.

Epomops franqueti (Tomes, 1860).—Jentink (1885:35, 1887:252, 1888:734) reports this species from Zemio, and Vielliard (1974:977) recorded it from "sud de la Republique Centre Africaine."

Scotonycteris zenkeri Matschie, 1894.—Vielliard (1974:977) recorded this species from "sud de la Republique Centre Africaine." Bergmans et al. (1974:38) reported three specimens from La Maboké, probably the same material referred to by Vielliard.

Nanonycteris veldkampii (Jentink, 1887).—This species was reported by Vielliard (1974:977) from "sud de la Republique Centre Africaine."

Myonycteris torquata (Dobson, 1878).—Vielliard (1974:977) reported this species from "sud de la Republique Centre Africaine." This locality is specified as La Maboké by Bergmans (1976:195).

Megaloglossus woermanni Pagenstecher, 1885.—Vielliard (1974:977) recorded this species from "sud de la Republique Centre Africaine."

Nycteris grandis Peters, 1871.—Blancou (1958:10) listed this species tentatively from Bangui.

Rhinolophus sp.—Blancou (1958:10) listed an unidentified *Rhinolophus* from Bozoum.

Chalinolobus variegatus (Tomes, 1861).—This species was listed from Zemio by Blancou (1958:10).

Kerivoula lanosa muscilla Thomas, 1906.—Hill (1977:627) reported a specimen reputedly from Bangui.

Tadarida condylura (A. Smith, 1833).—Blancou (1933:22) originally listed this species as *Nyctinomus angolensis* from the Ouaka and Kankja river valleys, but later he (Blancou, 1935:65–66) reported material from the same locality and from Grimari as *Tadarida condylura*.

Myopterus albatrus Thomas, 1915.—Malbrant (1952:213) noted that Blancou had obtained a bat of this genus at N'dele that could be either

M. albatrus or *M. whiteleyi* but was probably the former. Later Blancou (1958:10) listed "*Myotis* (*albatrus*?)" from N'dele.

DISCUSSION

The present paper brings to 45 the number of species of Chiroptera known from the Central African Republic. These are divided between those with affinities to the forest block of Central Equatorial Africa and those with affinities to the northern savannas. Only a single species, *Epomophorus pousarguesi*, is known at this time only from the Central African Republic, but it will undoubtedly be found in adjacent countries with additional collecting.

Some commonly occurring species of bats still have not been reported from the Central African Republic. These include, among others, such species as *Rousettus aegyptiacus*, *Taphozous nudiventris*, *Nycteris nana*, *N. macrotis*, *Rhinolophus clivosus*, *R. simulator*, *R. alcyon*, *Hipposideros caffer*, *H. cyclops*, *Pipistrellus kuhlii*, *P. ruepelli*, *Eptesicus capensis*, *E. rendalli*, *Nycticeius schlieffenii*, *Minioterus schreibersii*, *Tadarida aegyptiaca*, *T. major*, and *T. pumila*. In addition, some species with northern African or Palearctic affinities may also be found in the Central African Republic. This list would include *Rhinopoma microphyllum*, *R. hardwickei*, *Rhinolophus hipposideros*, *Pipistrellus deserti*, *Otonycteris hemprichii*, and *Plecotus austriacus*.

Judging from the number of species known from surrounding countries (but not yet known from the Central African Republic), it is probable that the list for this country is less than half complete. Kock (1969a) and Koopman (1975) have brought the known species of bats for the Sudan to 68 species. However, even in the Sudan, another 28 or more species might still be found to occur there. Therefore, for the Central African Republic, although most of the unreported species of bats should be found to occur in the southern forested portions of the country, many additional species with primarily Palearctic or savanna affinities might be found in the north. Additional collecting in all parts of the country should substantially increase the list of presently known species from this country.

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MORPHOMETRIC AND GEOGRAPHIC RELATIONSHIPS OF SHORT-TAILED SHREWS (GENUS *BLARINA*) IN KANSAS, IOWA, AND MISSOURI

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ABSTRACT

Shrews of the genus *Blarina* from Iowa, Kansas, and Missouri were studied morphometrically and karyologically. The ranges of two species, *B. brevicauda* and *B. hylophaga*, overlap in a broad zone across southern Iowa and northern Missouri. Morphometric analyses revealed an unexpectedly large amount of cranial variation in *B. brevicauda*, and confirmed the presence of that species in the Kansas River Valley of northeastern Kansas. Considerable mensural overlap was found in geographic areas in which *B. hylophaga* and *B. brevicauda* are sympatric, evincing the need for further karyotypic and morphometric studies in those areas. No formal taxonomic changes are proposed herein pending further study of these species.

INTRODUCTION AND TAXONOMIC HISTORY

Short-tailed shrews (genus *Blarina*) in Iowa, Kansas, Missouri, and surrounding states historically were assigned to subspecies of the species *Blarina brevicauda* (Say). Cockrum (1952:43), for example, recognized two subspecies of *B. brevicauda* in Kansas—*B. b. brevi-*

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cauda and *B. b. carolinensis* (Bachman). He stated that "Specimens of *B. b. breviceauda* from northeastern Kansas are measurably larger than specimens of *B. b. carolinensis* from southeastern Kansas. Specimens from intermediate geographic localities show a gradual gradation from one to the other—a cline in which no great step exists." Jones and Findley (1954) assigned all specimens they examined from Kansas to *B. b. carolinensis* and determined that the line of contact between *B. b. breviceauda* and *B. b. carolinensis* was in southern Nebraska rather than in Kansas. Jones and Glass (1960:137) studied additional western populations of short-tailed shrews and surmised that "A significant break does occur between shrews in southern Nebraska and those in central Nebraska and it is at this break that *B. b. breviceauda* is distinguished from specimens to the south. Shrews from southern Oklahoma to southern Nebraska seem to form a more or less natural grouping within the cline and in our judgement the same subspecific name [*B. b. carolinensis*] should be applied to all of them." This north-south cline in size was illustrated by Jones and Glass (1960:138) in their Fig. 1.

Referring to that figure, Jones (1964:30) noted that "shrews from Douglas County [in northeastern Kansas] and surrounding areas [sample E in Fig. 1, Jones and Glass, 1960:138] average appreciably larger cranially than shrews either to the north or south of them, and fit nearly perfectly as the missing middle segment into the otherwise sharply stepped north-south cline" Jones (1964:30) postulated that shrews from the Kansas River Valley of northeastern Kansas represented a remnant of "isolated populations of *B. breviceauda* that must have been left scattered in favorable places in the eastern part of the grasslands in the Xerothermic Period" In addition, Jones (1964:70) noted that the "external and cranial measurements of Nebraskan *carolinensis* do not differ appreciably . . . from the measurements of the type specimen of *Blarina breviceauda kirtlandi* Bole and Moulthrop"

Hoffmann and Jones (1970:389–390) detailed the apparent relationships among populations of *Blarina* on the Great Plains. They cited unpublished karyologic differences between northern and southern populations, which later were confirmed by Genoways et al. (1977), as support for the notion that two species of short-tailed shrews might be present on the Great Plains. Genoways and Choate (1972) subsequently published a multivariate analysis of populations of *Blarina* in Nebraska, and elevated *B. b. carolinensis* to the level of a species (*B. carolinensis*). In that study (Genoways and Choate, 1972:113), one specimen was identified as a possible hybrid whose "discriminant score . . . was nearer the upper limit for *carolinensis* than the lower limit for *breviceauda*"

Bowles (1975) assigned populations of short-tailed shrews in southwestern Iowa to the subspecies *B. b. carolinensis* even though Genoways and Choate (1972:114) had stated that "*brevicauda* and *carolinensis* behave as good biological species where their ranges are contiguous in [adjacent] southern Nebraska. Unpublished data (John B. Bowles, personal communication) indicate that a similar relationship between large and small phenotypes of *Blarina* probably exists across southern Iowa." Bowles (1975:34) did admit that the two taxa "seem to act more or less as distinct species where their ranges meet in southwestern Iowa." Later, Ellis et al. (1978) published a study of *Blarina* in Illinois. Their analyses indicated that *B. brevicauda* occurred nearly statewide, whereas *B. carolinensis* was present only in southernmost Illinois.

Despite morphometric (Jones and Glass, 1960; Jones, 1964; Genoways and Choate, 1972; Ellis et al., 1978) and karyologic (Genoways et al., 1977) evidence to the contrary, Hall (1981:54) recognized only one species of short-tailed shrew in central North America (*Blarina brevicauda*, consisting of the subspecies *B. b. brevicauda* and *B. b. carolinensis*) because Genoways and Choate (1972) had identified one of 66 specimens, from near the zone of contact of the two nominal taxa in Nebraska, as a probable hybrid or intergrade.

The genus *Blarina* long has been in need of taxonomic revision (Jones and Glass, 1960:140; Jones, 1964:69), and such a revision was begun by Genoways and Choate in 1965 when field studies to determine the status of *B. b. carolinensis* were conducted in southeastern Nebraska. Subsequently (in 1978), Genoways and Choate initiated extensive biochemical and morphometric investigations of all taxa of short-tailed shrews.

One of the problems to be resolved pertained to the relationships between eastern and western populations of *B. carolinensis*. Karyologic and morphometric analyses (George et al., 1981) resulted in resurrection of the name *Blarina hylophaga* Elliot (as predicted by Jones and Glass, 1960:140) for certain populations in Nebraska, Kansas, Iowa, Oklahoma, Arkansas, Missouri, Louisiana, and Texas previously known as *carolinensis*. In addition, those studies (George et al., 1982) confirmed the presence of *B. brevicauda* in Douglas County, Kansas (see Graham and Semken, 1976:439–440).

Another of the problems to be resolved pertained to the taxonomic and geographic relationships between *B. brevicauda* and *B. hylophaga* where the ranges of those species abut. In order to better understand those relationships, specimens were collected in 1979 and 1980 in southern Iowa (near the line of contact between the two taxa as described by Bowles, 1975) and in northern and central Missouri. Confirmation of the presence of *B. brevicauda* in the Kansas River Valley

(George et al., 1982), and the subsequent karyotyping (by NDM) of a specimen of *B. breviceauda* in Platte County, Missouri (across the Missouri River from the mouth of the Kansas River), led to incorporation of eastern Kansas into the geographic coverage of this study.

The objectives of this investigation, therefore, were to determine the geographic distributions of *B. breviceauda* and *B. hylophaga* in eastern Kansas, southern Iowa, and Missouri, and to elucidate their morphometric relationships. Because samples of *B. breviceauda* from those areas might pertain to either of two nominal subspecies (*B. b. breviceauda* or *B. b. kirtlandi*), comparisons are made with reference samples of both taxa. Herein, the three taxa are referred to as *hylophaga*, *breviceauda*, and *kirtlandi*. Another species, *B. carolinensis*, is known from the "bootheel" region of Missouri and the Mississippi floodplain near St. Louis, Missouri (George et al., 1981), but is not considered in this study.

MATERIALS AND METHODS

A total of 851 specimens from Illinois, Iowa, Kansas, Missouri, Nebraska, Ohio, and Oklahoma was examined. These specimens are deposited in the following collections: Carnegie Museum of Natural History (CM); Cleveland Museum of Natural History (CMNH); Central College, Iowa (CUI); Pittsburg State University, Kansas (KSCP); Museum of Natural History, University of Kansas (KU); Museum of the High Plains, Fort Hays State University (MHP); Minnesota Museum of Natural History, University of Minnesota (MMNH); University of Missouri (MOU); Museum of Natural and Cultural History, Oklahoma State University (OSU); Stovall Museum of Science and History, University of Oklahoma (OU); Royal Ontario Museum (ROM); Sherman Hoslett Memorial Museum of Natural History, Luther College, Iowa (SHMC); University of Colorado Museum (UCM); University of Michigan Museum of Zoology (UMMZ); National Fish and Wildlife Laboratory, National Museum of Natural History (USNM); Museum of Natural History, University of Wisconsin-Stevens Point (UWSP).

The following cranial and mandibular measurements (Choate, 1972) were taken with dial calipers to the nearest 0.1 mm and recorded for each specimen: occipito-premaxillary length (OPLN); P⁴-M³ length (PMLN); cranial breadth (CRNBR); breadth of zygomatic plate (ZYPBR); maxillary breadth (MAXBR); interorbital breadth (INOBR); length of mandible (LENMA); height of mandible (HEMAN); and articular breadth (ARTBR). Specimens were assigned to age classes on the basis of wear to teeth and condition of pelage (Choate, 1972; see also Choate, 1968). Only those specimens with complete sets of cranial and mandibular measurements were used in statistical analyses, which were performed via remote hookup with the ITTEL AS/5 at Kansas State University.

Tests for non-geographic variation revealed no consistent pattern of significant differences among age classes and no statistically significant differences among sex classes. Choate (1972) carefully assessed secondary sexual and age variation within populations of *Blarina* in Connecticut and combined age and sex classes for further analyses. Because of Choate's (1972) findings and the lack of a consistent pattern of significant differences in these tests, all age and sex classes were pooled for subsequent statistical analyses.

Assignment of unknowns to reference samples of *breviceauda*, *hylophaga*, and *kirtlandi* was necessary before conducting further statistical analyses. The cluster analysis

(UPGMA) of the Numerical Taxonomic System (NT-SYS, Rohlf et al., 1974) was found to be unsuitable for this task because initial runs (using individuals as OTUs) clustered reference samples of *kirtlandi* from Ohio with *hylophaga* from western Kansas. S. B. George (personal communication) obtained similar results using the DISCRIMINANT procedure of the Statistical Package for the Social Sciences (SPSS, Nie et al., 1975); that procedure was unable to discriminate between samples of *hylophaga* from eastern Kansas and *kirtlandi* from Ohio. A second run of the UPGMA procedure clustered a reference sample of *kirtlandi* from Illinois with *hylophaga* from western Kansas.

At this point, the DISCRIMINANT procedure of the Statistical Analysis System (SAS) 79.3A (Helwig and Council, 1979) was employed because of its greater discriminating capability. Four hundred seventy-nine unknowns from Iowa, Kansas, and Missouri were assigned to reference samples of *B. brevicauda* from Nebraska and *B. hylophaga* from Kansas using this procedure. Preliminary examination of skulls had revealed extensive cranial variation in unknowns from Iowa and Missouri assigned to *B. brevicauda*; specimens as large as topotypical *brevicauda* and as small as topotypical *kirtlandi*, with all gradations between, were present. Because of this variation and the results of analysis by NT-SYS, reference samples of *kirtlandi* were omitted to increase the discriminating power of this procedure (reference samples of *kirtlandi* were used in all subsequent analyses). Additionally, topotypical specimens of *hylophaga* were not used in reference samples because *hylophaga* varies geographically (as described by George et al., 1981) and specimens from near the type locality in southern Oklahoma are considerably smaller than specimens from Iowa, Kansas, and Missouri.

In order to represent geographic variation within *B. brevicauda* and *B. hylophaga* in subsequent analyses, three additional reference samples were selected. This resulted in a total of five reference samples of three taxa of *Blarina* from the following counties (sample sizes are indicated in parentheses): *B. b. brevicauda*, Nebraska—Boyd, Burt, Butler, Cedar, Cherry, Holt, Knox, Washington, and Wayne (25); *B. brevicauda*, Iowa—Chickasaw, Howard, and Winneshiek (28); *B. b. kirtlandi*, Ohio—Geauga and Lake (23); *B. hylophaga*, Kansas—Ellis, Osborne, Phillips, Rooks, Rush, Russell, and Trego (26); *B. hylophaga*, Oklahoma—Cleveland, Garvin, McClain, Murray, and Payne (28). Herein, these samples are identified by the numbers 23, 24, 25, 26, and 27, respectively.

Standard statistics (mean, standard error, range, and coefficient of variation) were computed for each mensural character by sample, and a Duncan's multiple range test was performed for each character. The MANOVA option of the GLM procedure of SAS was used to compute characteristic roots and vectors that were used later in a canonical (discriminant) analysis of variation within and among samples (methodology described by Yates and Schmidly, 1977:5).

Because species of *Blarina* previously have been characterized by their karyotypes (George et al., 1982), karyotypes were prepared to confirm identification based on morphometric analyses. Eight specimens (MHP numbers in parentheses) from the following localities were karyotyped as described by Baker (1970): Kansas—Douglas County: 2½ mi. N, ½ mi. E Lawrence, T.12S, R.20E, W ½ sec. 20 (18806, 18807); Douglas County: 2 mi. N, 1½ mi. E Lawrence, T.12S, R.20E, SE ¼ sec. 20 (17702, 17879); Osage County: 1 mi. S, 4 mi. E Scranton, T.15S, R.16E, NE ¼ sec. 7 (18809, 18810, 18811); and Missouri—Platte County: ¼ mi. N, 1 mi. W Weston, T.53N, R.36W, NW ¼ sec. 10 (18808).

RESULTS

The DISCRIMINANT procedure of SAS assigned 183 unknowns to *B. brevicauda* and 296 unknowns to *B. hylophaga*. After assignment to reference samples, specimens from proximal trapping localities were

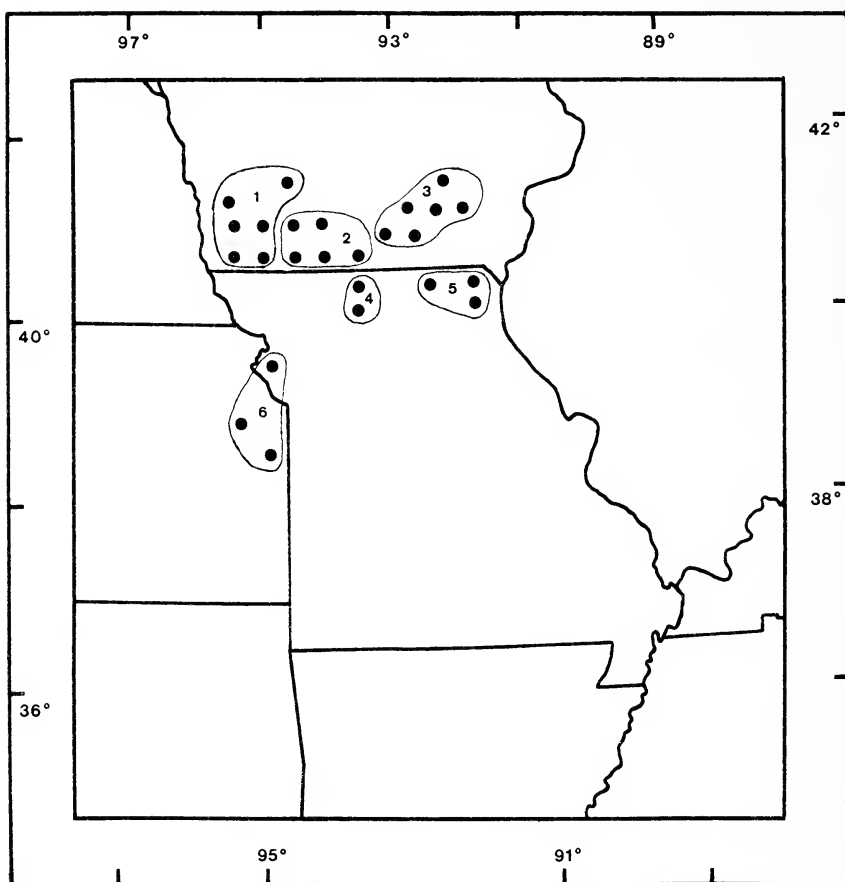


Fig. 1.—Geographic distribution of pooled samples assigned to *Blarina brevicauda*. Numbers refer to samples in Appendix 1.

pooled to increase sample sizes and the discriminating power of univariate and multivariate analyses. A total of 22 samples resulted from this pooling. Samples 1–6 (Fig. 1) include specimens assigned to *B. brevicauda*; samples 7–22 (Fig. 2) consist of specimens assigned to *B. hylophaga* (see Appendix 1 for a listing of sample sizes and counties included within each sample). Eleven specimens were assigned to *B. brevicauda* with less than 0.95 posterior probability of correct assignment; eight specimens were assigned to *B. hylophaga* with a posterior probability of correct assignment of less than 0.95. Trapping localities

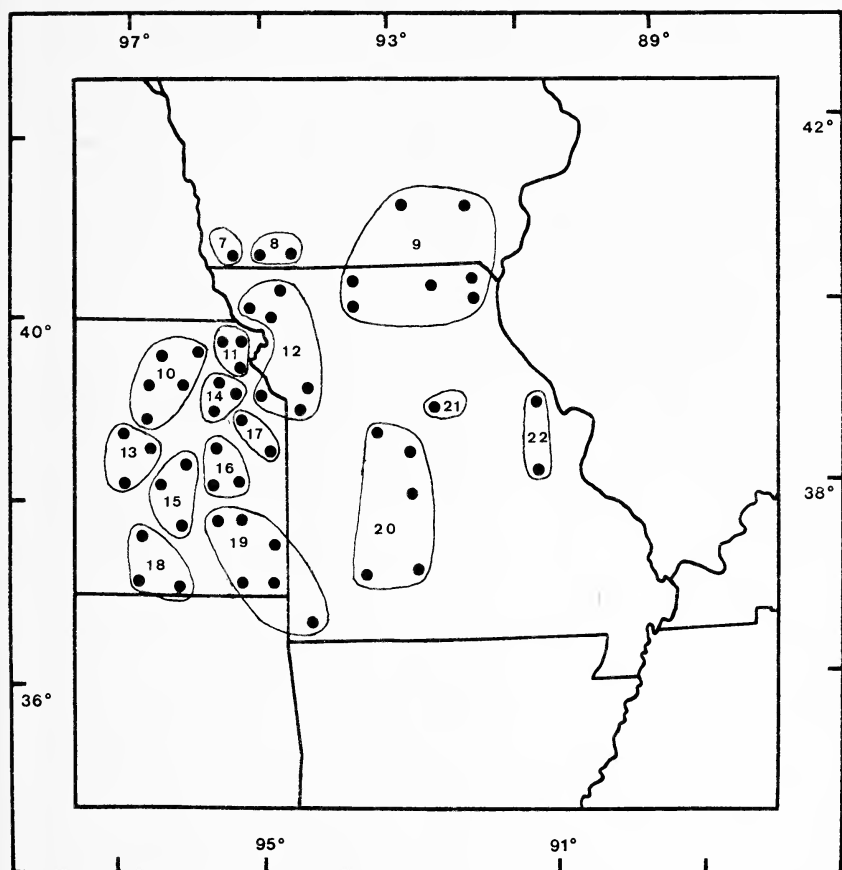


Fig. 2.—Geographic distribution of pooled samples assigned to *Blarina hylophaga*. Numbers refer to samples in Appendix 1.

that contained specimens assigned to both species were located in the following counties (see Fig. 3); samples numbers are identified in parentheses: Iowa—Fremont (1, 7), Keokuk (3, 9), Marion (3, 9), Page (1, 8), Taylor (2, 8); Kansas—Douglas (6, 17), Miami (6, 17); Missouri—Adair (5, 9), Clark (5, 9), Grundy (4, 9), Lewis (5, 9), Mercer (4, 9).

Four routines of MANOVA were used to test the hypothesis that there are no significant morphometric differences among samples. Each of the four tests had results which were significant at $P < 0.0001$:

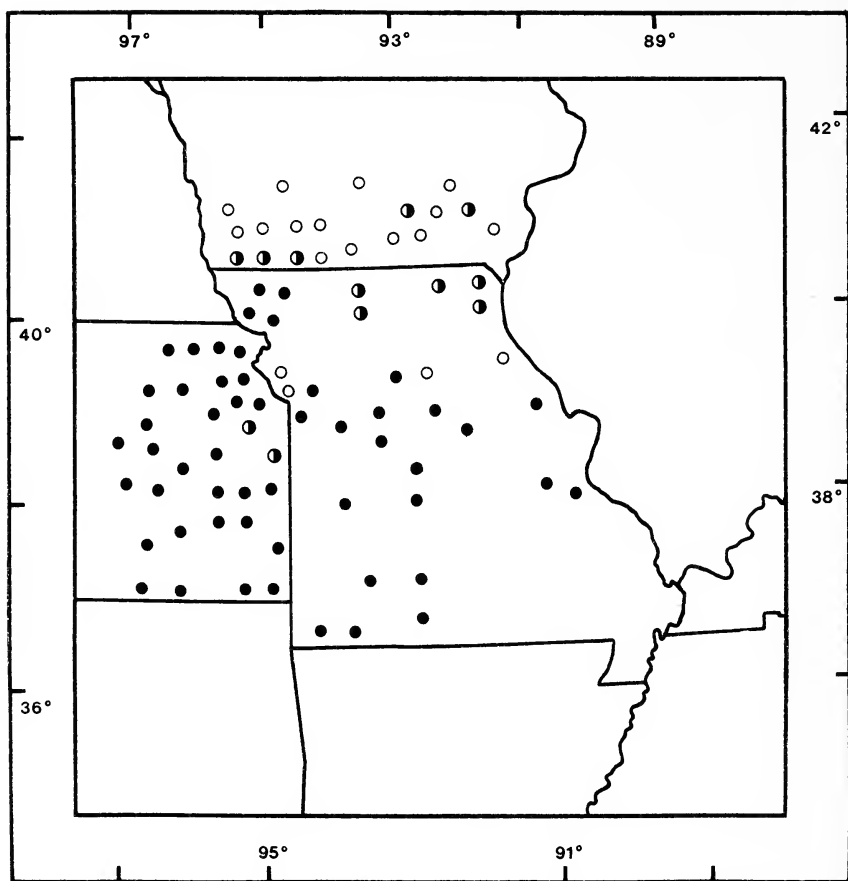


Fig. 3.—Partial geographic distribution of *Blarina brevicauda* and *B. hylophaga* in Kansas, Iowa, and Missouri. Open circles represent counties from which all specimens were assigned to *B. brevicauda*; solid circles represent counties from which all specimens were assigned to *B. hylophaga*; half-solid circles represent counties from which specimens assigned to both species were collected at the same trapping locality. See specimens examined for exact localities.

Hotelling-Lawley's Trace ($F = 21.39$); Pillai's Trace ($F = 5.34$); Wilk's Criterion ($F = 9.22$); Roy's Maximum Root Criterion ($F = 172.28$).

Table 1 lists standard statistics for all characters and illustrates the results of the Duncan's multiple range tests. For each character, analysis of variance revealed highly significant differences ($P < 0.001$) among samples.

Table 1.—Univariate statistics for all samples by mensural character. Reference samples mentioned in text are indicated with an asterisk. Samples are identified in Appendix 1. Vertical lines represent nonsignificant subsets as determined by Duncan's multiple range tests; each line represents a separate subset and vertical positioning of lines is insignificant. *F* value for each character is indicated in parentheses.

Sample	Mean	2 SE	Range	CV	N
<i>Occipito-premaxillary length</i> (<i>F</i> = 119.56)					
23*	24.00	0.22	23.1–25.2	2.26	25
3	23.58	0.13	22.6–24.8	2.21	62
1	23.51	0.22	21.8–24.6	2.58	30
2	23.41	0.18	20.6–24.9	2.98	56
24*	23.32	0.31	21.7–24.6	3.57	28
5	22.97	0.32	22.3–23.7	2.22	10
4	22.97	0.27	22.0–24.5	2.67	20
6	22.36	0.20	22.0–22.6	1.03	5
9	22.30	0.24	21.6–22.9	1.82	11
17	21.87	0.12	20.3–22.7	2.07	54
25*	21.50	0.23	20.8–23.0	2.66	23
21	21.29	0.18	20.6–22.1	2.05	23
22	21.23	0.46	20.4–22.0	2.64	6
12	21.23	0.28	19.9–22.1	2.89	19
8	21.01	0.26	20.2–22.3	2.84	21
11	20.98	0.29	19.7–21.5	2.47	13
7	20.94	0.15	19.6–22.3	2.55	47
26*	20.90	0.16	20.2–21.7	1.93	26
20	20.90	0.31	20.1–21.2	1.95	7
16	20.87	0.32	20.0–21.7	2.55	11
10	20.85	0.17	20.2–20.5	1.85	20
15	20.71	0.17	19.7–21.6	2.16	27
18	20.69	0.36	20.1–21.7	2.51	8
14	20.65	0.43	19.4–21.5	3.28	10
19	20.63	0.24	19.9–21.4	2.04	12
13	20.54	0.21	20.1–20.8	1.40	7
27*	20.01	0.18	18.8–21.0	2.42	28

The variance-covariance matrix yielded nine canonical variates among the nine mensural characters for all 27 samples. The first canonical variate expressed 88.00% of the morphometric variation, the second 4.52%, and the third 3.20%. Two-dimensional plots of the first two canonical variates (Fig. 4; an ellipse encloses the mean and one standard deviation on each side of the mean for each sample) yielded results similar to those of the Duncan's multiple range tests: sample 23 (reference for *brevicauda* from Nebraska) was placed at the top of the plot and sample 27 (reference for *hylophaga* from Oklahoma) was placed at the bottom of the plot along vector 1, which primarily reflects size variation; sample 6 (*brevicauda*) clustered with samples 1–5 (*brev-*

Table 1.—*Continued.*

Sample	Mean	2 SE	Range	CV	N
<i>P⁴-M³ length (F = 73.54)</i>					
23*	6.59	0.06	6.3-6.8	2.33	25
1	6.46	0.08	5.8-6.8	3.65	30
3	6.45	0.04	6.1-6.8	2.79	62
2	6.43	0.04	6.0-6.8	2.66	56
24*	6.40	0.08	5.8-6.9	3.55	28
5	6.26	0.14	5.9-6.6	3.47	10
6	6.24	0.10	6.1-6.4	1.83	5
4	6.20	0.08	5.9-6.5	2.79	20
9	6.15	0.13	5.7-6.5	3.51	11
17	6.14	0.04	5.6-6.4	2.71	54
22	5.88	0.12	5.7-6.1	2.50	6
21	5.86	0.07	5.6-6.2	2.76	23
25*	5.86	0.05	5.6-6.0	2.40	23
11	5.84	0.10	5.4-6.1	3.01	13
12	5.80	0.12	5.1-6.2	4.46	19
10	5.79	0.04	5.6-6.0	1.72	20
16	5.79	0.06	5.7-6.0	1.80	11
20	5.79	0.18	5.4-6.0	4.17	7
7	5.79	0.05	5.5-6.3	3.26	47
8	5.77	0.08	5.5-6.3	3.25	21
14	5.76	0.10	5.5-6.0	2.74	10
26*	5.74	0.07	5.3-6.2	3.31	26
18	5.72	0.15	5.4-6.0	3.70	8
15	5.71	0.06	5.4-6.0	2.97	27
13	5.69	0.10	5.5-5.9	2.37	7
19	5.64	0.10	5.3-5.9	3.07	12
27*	5.55	0.06	5.2-5.9	3.04	28

icauda) and 24 (reference for *B. brevicauda* from Iowa), and was placed below those samples along vector 1; samples 9 and 17 (*hylophaga*) overlapped each other slightly at the upper end of the lower cluster and were positioned between samples 24 (reference for *B. brevicauda* from Iowa) and 25 (reference for *kirtlandi* from Ohio) along vector 1; sample 25 did not cluster with other samples of *B. brevicauda* (1-6, 23, and 24); reference samples were arranged along vector 1 from highest to lowest in the order 23, 24, 25, 26, and 27; samples 7, 8, 10, 11, 13-16, 18, 19, and 26 (*hylophaga*) clustered together and overlapped so greatly that individual ellipses were essentially indistinguishable; sample 27 (reference for *hylophaga* from Oklahoma) clustered with other samples of *hylophaga* but did not overlap appreciably with any of them.

Karyotypes of specimens from Douglas County, Kansas, and Platte

Table 1.—*Continued.*

Sample	Mean	2 SE	Range	CV	N
<i>Cranial breadth</i> ($F = 99.63$)					
23*	13.51	0.14	12.6–14.0	2.57	25
1	13.22	0.18	11.7–13.9	3.75	30
2	13.19	0.12	12.2–14.1	3.48	56
3	13.17	0.10	12.0–14.0	2.99	62
24*	13.13	0.22	12.0–14.2	4.38	28
4	12.88	0.21	12.0–14.0	3.67	20
5	12.78	0.13	12.5–13.2	1.64	10
6	12.58	0.28	12.2–13.0	2.54	5
9	12.51	0.20	12.0–13.0	2.69	11
17	12.23	0.09	11.2–12.8	2.86	54
25*	12.04	0.10	11.5–12.6	2.24	23
21	12.01	0.15	11.4–12.8	3.09	23
22	11.98	0.25	11.6–12.4	2.55	6
20	11.80	0.21	11.3–12.2	2.35	7
12	11.78	0.20	11.0–12.5	3.68	19
8	11.63	0.18	10.9–12.6	3.69	21
7	11.52	0.10	10.8–12.3	2.92	47
11	11.45	0.19	10.9–12.0	3.08	13
26*	11.45	0.12	10.8–11.9	2.66	26
10	11.40	0.15	10.6–11.8	3.00	20
16	11.37	0.17	10.9–12.0	2.46	11
13	11.34	0.19	10.9–11.7	2.21	7
14	11.34	0.36	10.3–12.2	5.01	10
18	11.31	0.21	10.9–11.9	2.65	8
19	11.31	0.26	10.8–12.2	4.05	12
15	11.24	0.14	10.6–12.3	3.36	27
27*	10.96	0.11	10.3–11.6	2.70	28

County, Missouri, evinced that those specimens pertained to *B. brevicauda* ($2N = 48, 49$, or 50 ; $FN = 48$). Examination of skulls of those individuals indicated that they were near the upper mensural extreme for *hylophaga* (and, therefore, near the lower limit of cranial variation for *kirtlandi*), but certain cranial characteristics (for example, shape of the braincase) were more like those of *kirtlandi* than of *hylophaga*. Those specimens thus were assigned to the species *B. brevicauda* on the basis of both morphometric and karyologic evidence. Karyotypes of specimens from Osage County, Kansas, confirmed that those specimens pertained to *B. hylophaga* ($2N = 52$; $FN = 60, 61$, or 62).

DISCUSSION

Specimens of the genus *Blarina* traditionally have been assigned taxonomically on the basis of external and cranial measurements (Bole

Table 1.—Continued.

Sample	Mean	2 SE	Range	CV	N
<i>Breadth of the zygomatic plate ($F = 26.15$)</i>					
23*	2.71	0.09	2.3–3.1	7.97	25
5	2.68	0.09	2.4–2.9	5.22	10
2	2.65	0.06	2.1–3.2	7.89	56
9	2.64	0.11	2.4–3.0	7.24	11
1	2.63	0.06	2.4–2.9	5.83	30
24*	2.61	0.06	2.2–2.9	5.84	28
3	2.60	0.06	2.0–2.9	8.09	62
4	2.60	0.12	2.1–3.2	10.14	20
17	2.51	0.05	2.0–3.0	7.27	54
21	2.45	0.07	2.2–2.7	6.73	23
6	2.44	0.16	2.2–2.6	7.44	5
20	2.39	0.08	2.2–2.5	4.48	7
12	2.33	0.08	2.1–2.6	7.14	19
25*	2.33	0.06	2.0–2.6	5.97	23
22	2.32	0.18	2.0–2.6	9.62	6
13	2.31	0.12	2.2–2.6	5.81	7
7	2.29	0.05	1.8–2.6	7.01	47
11	2.25	0.10	2.0–2.5	7.81	13
19	2.24	0.09	2.0–2.5	6.71	12
26*	2.24	0.05	2.0–2.5	5.52	26
8	2.24	0.08	1.8–2.5	8.17	21
18	2.22	0.10	2.0–2.5	6.69	8
15	2.21	0.06	1.8–2.5	6.64	27
10	2.20	0.05	2.0–2.4	5.40	20
14	2.18	0.11	2.0–2.5	8.03	10
16	2.16	0.10	1.9–2.4	7.53	11
27*	2.13	0.06	1.8–2.4	7.34	28

and Moulthrop, 1942; Cockrum, 1952; Jones and Glass, 1960; Jones, 1964; Genoways and Choate, 1972; Bowles, 1975; Ellis et al., 1978; George et al., 1981). Jones and Glass (1960:137) asserted that "Size . . . [in *Blarina*] definitely varies geographically and seems to be a . . . useful criterion in taxonomic studies."

The mensural relationship between *B. brevicauda brevicauda* and *B. hylophaga* is distinctive: "*Blarina brevicauda brevicauda* can be distinguished from *B. b. carolinensis* [= *B. hylophaga*] . . . by its markedly greater external and cranial size" (Bowles, 1975:34); "*B. b. brevicauda* . . . differs [from *B. hylophaga*] in being significantly larger externally and especially cranially" (Jones, 1964:67); "external and cranial dimensions in *B. b. brevicauda* are substantially greater than (and seldom overlap) those in *B. b. carolinensis* [= *B. hylophaga*]" (Genoways and Choate, 1972:106–107). However, the mensural

Table 1.—*Continued.*

Sample	Mean	2 SE	Range	CV	N
<i>Maxillary breadth (F = 84.02)</i>					
23*	8.66	0.10	8.0–9.1	2.79	25
1	8.56	0.10	8.0–9.0	3.22	30
2	8.49	0.07	7.7–9.2	3.23	56
3	8.47	0.06	8.0–9.0	2.83	62
24*	8.32	0.12	7.7–8.9	3.94	28
4	8.28	0.17	7.6–9.2	4.53	20
5	8.20	0.18	7.8–8.7	3.50	10
6	8.08	0.40	7.6–8.6	5.49	5
9	7.93	0.13	7.5–8.3	2.83	11
17	7.75	0.06	7.3–8.3	2.69	54
8	7.61	0.16	7.1–8.4	4.88	21
26*	7.58	0.08	7.1–7.9	2.65	26
12	7.58	0.10	7.1–8.0	3.08	19
22	7.58	0.21	7.3–8.0	3.48	6
25*	7.55	0.10	7.1–7.8	3.29	23
21	7.51	0.09	7.2–7.9	2.81	23
11	7.50	0.07	7.2–7.7	1.63	13
7	7.48	0.08	6.9–8.3	3.87	47
10	7.45	0.10	7.1–7.8	2.90	20
16	7.45	0.14	7.2–7.9	3.14	11
13	7.43	0.12	7.2–7.7	2.16	7
20	7.43	0.17	7.0–7.7	3.08	7
19	7.35	0.10	7.1–7.6	2.28	12
14	7.33	0.15	7.0–7.8	3.28	10
15	7.31	0.09	6.6–7.7	3.36	27
18	7.22	0.12	6.8–7.4	2.64	8
27*	7.15	0.09	6.7–7.8	3.28	28

distinction between *B. brevicauda kirtlandi* (which Bole and Moulthrop, 1942:100, described as being “intermediate between other forms . . .”) and *B. hylophaga* is slight, and the extremes of variation in these taxa overlap broadly, as do the extremes of variation between *B. b. brevicauda* and *B. b. kirtlandi* (see Graham and Semken, 1976). As depicted by Hall (1981:55), the range of *B. b. carolinensis* west of the Mississippi River [= *B. hylophaga*] is separated geographically from that of *B. b. kirtlandi* so that the lack of mensural distinction between the two taxa is of little consequence. However, Ellis et al. (1978:310) examined specimens of *B. brevicauda* from Illinois and central Iowa and concluded “there is a step within this cline [between *brevicauda* and *kirtlandi*] somewhere along the Mississippi River, between northwestern Illinois and central Iowa . . .” They did not examine specimens between northwestern Illinois and central Iowa, but

Table 1.—Continued.

Sample	Mean	2 SE	Range	CV	N
<i>Interorbital breadth (F = 40.96)</i>					
23*	6.18	0.09	5.9–6.7	3.51	25
1	6.14	0.08	5.7–6.8	3.86	30
2	6.12	0.06	5.7–6.5	3.31	56
3	6.11	0.05	5.6–6.5	3.10	62
24*	6.05	0.09	5.6–6.5	4.06	28
4	5.99	0.10	5.6–6.6	3.86	20
5	5.98	0.11	5.8–6.3	2.93	10
9	5.91	0.09	5.6–6.2	2.67	11
17	5.85	0.05	5.5–6.2	3.06	54
6	5.84	0.12	5.7–6.0	2.30	5
21	5.75	0.08	5.5–6.3	3.27	23
8	5.73	0.08	5.4–6.0	3.32	21
12	5.72	0.08	5.4–6.1	3.22	19
7	5.66	0.06	5.2–6.0	3.48	47
22	5.62	0.17	5.3–5.9	3.80	6
26*	5.61	0.05	5.4–5.9	2.33	26
16	5.59	0.09	5.4–5.8	2.82	11
20	5.59	0.18	5.2–5.9	4.31	7
10	5.57	0.08	5.1–5.8	3.44	20
14	5.56	0.08	5.4–5.8	2.43	10
13	5.56	0.07	5.5–5.7	1.76	7
11	5.55	0.08	5.2–5.8	2.72	13
19	5.53	0.10	5.3–5.8	3.11	12
15	5.52	0.04	5.4–5.7	1.74	27
25*	5.52	0.05	5.3–5.8	2.30	23
18	5.51	0.11	5.3–5.8	2.82	8
27*	5.41	0.06	5.1–5.9	3.18	28

their conclusion allowed for the possibility that two very similar taxa (*B. b. kirtlandi* and *B. hylophaga*) occur together in Iowa and, perhaps, Missouri. Data presented herein are inadequate to judge the taxonomic status of the two subspecies of *B. brevicauda*, but they indicate that mensural variation in samples of *B. brevicauda* from Missouri and southern Iowa is not merely a function of geography. Specimens from the same trapping localities often exhibit variation ranging from that of large *brevicauda* to that of small *kirtlandi*, including intermediate-sized shrews. In fact, *kirtlandi*-sized specimens of *B. brevicauda* exist as far west as eastern Nebraska. This might explain the specimen described by Genoways and Choate (1972:113) as a possible hybrid; that specimen was slightly smaller than topotypical *brevicauda* but slightly larger than specimens of *hylophaga* from southeastern Nebraska, as are specimens of *kirtlandi*. On the other hand, specimens

Table 1.—*Continued.*

Sample	Mean	2 SE	Range	CV	N
<i>Length of the mandible (F = 108.92)</i>					
23*	13.79	0.12	13.3–14.4	2.10	25
3	13.58	0.09	13.0–14.2	2.56	62
2	13.53	0.11	12.6–14.3	3.12	56
1	13.48	0.14	12.6–14.3	3.04	30
24*	13.35	0.19	12.3–14.2	3.79	28
4	13.10	0.21	12.2–14.1	3.57	20
5	13.06	0.21	12.6–13.6	2.61	10
6	12.78	0.12	12.7–13.0	1.02	5
9	12.71	0.16	12.3–13.0	2.15	11
17	12.66	0.08	11.8–13.1	2.30	54
21	12.13	0.12	11.6–12.5	2.31	23
25*	12.10	0.16	11.6–13.0	3.16	23
12	12.08	0.20	11.3–12.8	3.70	19
22	12.07	0.28	11.6–12.5	2.90	6
20	12.06	0.32	11.3–12.6	3.55	7
8	12.04	0.18	11.5–13.0	3.52	21
7	11.97	0.10	11.3–12.9	2.93	47
26*	11.93	0.12	11.4–12.6	2.65	26
11	11.91	0.16	11.2–12.3	2.39	13
10	11.86	0.11	11.3–12.2	2.18	20
16	11.83	0.19	11.2–12.5	2.73	11
15	11.79	0.13	11.0–12.5	2.86	27
18	11.74	0.15	11.5–12.1	1.87	8
13	11.73	0.19	11.3–12.1	2.13	7
14	11.68	0.26	11.0–12.5	3.49	10
19	11.67	0.14	11.2–12.1	2.11	12
27*	11.30	0.11	10.7–12.0	2.70	28

of *hylophaga* from southeastern Nebraska examined by Jones (1964:70) actually were individuals of that species that merely had cranial measurements near the upper extreme for *hylophaga*. Jones' (1964:70) statement about the mensural relationships between those specimens and the holotype of *kirtlandi* concur with observations, made by Graham and Semken (1976), about the overlapping mensural extremes of these taxa.

Results of the Duncan's multiple range tests (Table 1) and the canonical analysis (Fig. 4) illustrate cranial variation within test samples of *B. brevicauda* from Iowa and Missouri: samples 1–5 had larger means than sample 25 (reference for *kirtlandi* from Ohio) but had smaller means than sample 23 (reference for *brevicauda* from Nebraska) and clustered with the reference for *B. brevicauda* from Iowa (sample 24). Examination of Table 1 reveals that, for all characters except

Table 1.—Continued.

Sample	Mean	2 SE	Range	CV	N
<i>Height of the mandible (F = 134.02)</i>					
23*	7.86	0.09	7.4–8.2	2.91	25
2	7.66	0.08	6.8–8.3	4.33	56
1	7.63	0.10	7.2–8.1	3.56	30
3	7.61	0.06	7.2–8.2	3.01	62
24*	7.51	0.16	6.2–8.4	5.80	28
4	7.45	0.15	6.9–8.2	4.49	20
5	7.33	0.16	7.0–7.8	3.52	10
6	7.10	0.18	6.9–7.4	2.82	5
9	7.04	0.06	6.9–7.2	1.46	11
17	6.81	0.06	6.1–7.2	3.34	54
22	6.65	0.25	6.3–7.1	4.63	6
25*	6.64	0.09	6.3–7.1	3.17	23
12	6.55	0.15	5.9–7.0	5.04	19
21	6.55	0.10	6.2–7.1	3.82	23
20	6.47	0.20	5.9–6.7	4.16	7
8	6.36	0.16	5.9–7.2	5.91	21
11	6.28	0.09	5.9–6.5	2.53	13
26*	6.26	0.07	5.8–6.5	2.99	26
7	6.25	0.08	5.8–7.1	4.18	47
16	6.19	0.11	5.9–6.5	3.10	11
15	6.16	0.10	5.7–6.7	4.22	27
14	6.15	0.24	5.7–6.9	6.14	10
19	6.14	0.09	5.9–6.4	2.64	12
10	6.13	0.08	5.8–6.5	3.00	20
13	6.11	0.19	5.8–6.4	4.27	7
18	6.04	0.18	5.8–6.6	4.24	8
27*	5.90	0.08	5.5–6.4	3.49	28

two (ZYPBR and ARTBR), sample 24 (*B. brevicauda* from Iowa) had the highest coefficient of variation of any of the reference samples. These observations, together with the placement of samples 1–5 and 24 in the canonical analysis between sample 23 (*brevicauda* from Nebraska) and sample 25 (*kirtlandi* from Ohio) along vector 1 (Fig. 4), indicate that samples 1–5 and 24 contained *brevicauda*- and *kirtlandi*-sized shrews as well as intermediate-sized individuals. The fact that this variation is non-geographic, and the fact that no indication of secondary intergradation (for example, a step) between *brevicauda* and *kirtlandi* has been found either east or west of areas included in this study, preclude assigning specimens of *B. brevicauda* from Iowa, Kansas, and Missouri to either *B. b. brevicauda* or *B. b. kirtlandi* until completion of an ongoing investigation of geographic variation within the overall range of the species. Nevertheless, sample 6, from Kansas

Table 1.—*Continued.*

Sample	Mean	2 SE	Range	CV	N
<i>Articular breadth (F = 90.60)</i>					
23*	2.98	0.04	2.8–3.2	3.40	25
1	2.87	0.06	2.6–3.2	5.50	30
2	2.84	0.04	2.3–3.5	6.29	56
5	2.76	0.07	2.6–3.0	3.89	10
3	2.75	0.03	2.5–3.0	4.95	62
24*	2.75	0.05	2.5–3.0	4.80	28
4	2.75	0.07	2.5–3.2	5.60	20
6	2.62	0.07	2.5–2.7	3.19	5
9	2.54	0.07	2.4–2.7	4.75	11
17	2.46	0.03	2.2–2.7	4.55	54
25*	2.43	0.04	2.3–2.7	4.40	23
22	2.43	0.10	2.3–2.6	4.98	6
20	2.41	0.07	2.3–2.5	3.73	7
21	2.41	0.05	2.2–2.6	4.56	23
12	2.38	0.06	2.1–2.6	5.16	19
8	2.33	0.08	2.1–2.7	7.71	21
7	2.29	0.04	2.0–2.7	5.99	47
15	2.27	0.05	2.0–2.5	5.87	27
26*	2.26	0.04	2.1–2.4	4.69	26
11	2.25	0.06	2.0–2.4	4.66	13
10	2.24	0.05	2.0–2.4	5.10	20
18	2.24	0.05	2.1–2.3	3.32	8
13	2.21	0.10	2.1–2.4	6.07	7
14	2.21	0.09	2.1–2.5	6.56	10
19	2.21	0.07	2.0–2.4	5.27	12
16	2.18	0.04	2.1–2.3	3.44	11
27*	2.10	0.04	1.9–2.4	5.73	28

and Missouri, was placed nearer sample 25 (reference for *kirtlandi* from Ohio) than sample 23 (reference for *brevicauda* from Nebraska) in the canonical analysis (Fig. 4), and had the smallest mean of any of the samples of *B. brevicauda* (other than sample 25) in eight of nine range tests (Table 1). These analyses, together with karyotypic data and cranial appearance as determined by examination of skulls, indicate that populations of *B. brevicauda* are present in Douglas and Miami counties, Kansas, and Buchanan and Platte counties, Missouri, and that they are more similar to *kirtlandi* than to *brevicauda* (as pointed out previously by Graham and Semken, 1976).

Statistical analyses and examination of skulls of specimens of *hylophaga* revealed considerable geographic variation in size within that species, as reported by George et al., (1981); specimens of *hylophaga* from Oklahoma (sample 27) were near *B. carolinensis* in size and were

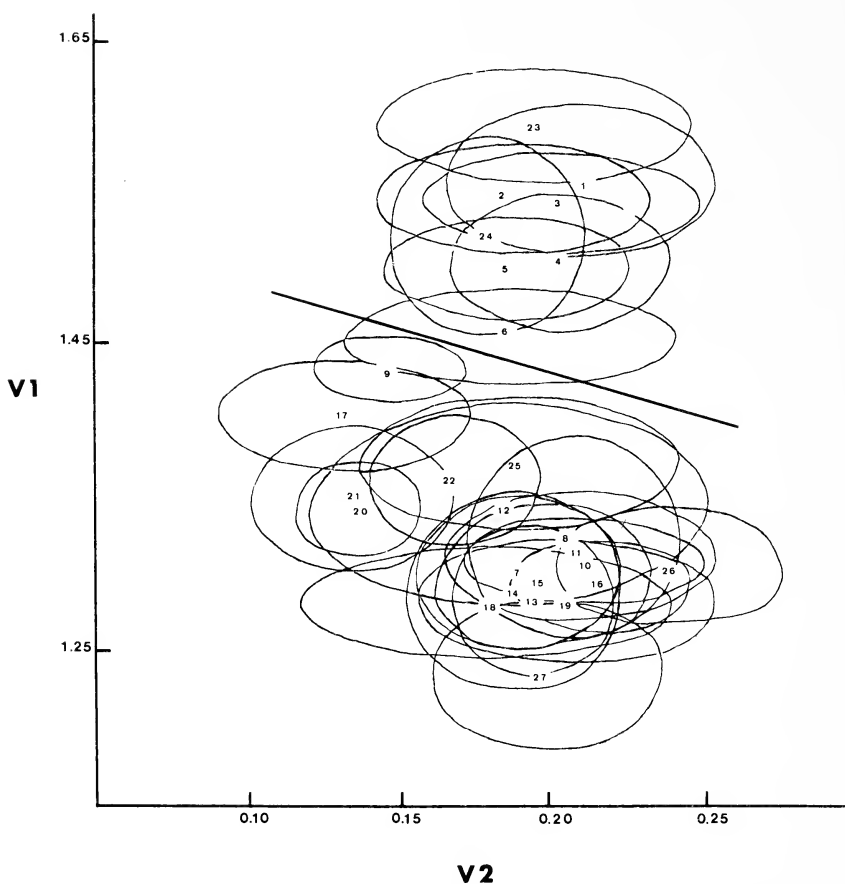


Fig. 4.—Canonical analysis of all samples. Samples 1–6 were assigned to *Blarina brevicauda*; samples 7–22 were assigned to *B. hylophaga*. Samples 23–25 were used as references for *B. brevicauda*; samples 26 and 27 were used as references for *B. hylophaga*.

smaller than test specimens of *hylophaga* from Iowa, Kansas, and Missouri. Certain test samples of *hylophaga* (9, 12, 17, and 20–22) were placed nearer toptotypical specimens of *kirtlandi* (sample 25) than the references for *hylophaga* (samples 26 and 27) by the canonical analysis (Fig. 4), thus reiterating the mensural similarities between toptotypical *kirtlandi* and western populations of *hylophaga* as revealed in this study by the NT-SYS cluster analysis and as noted by Jones (1964:70).

Because of these mensural similarities, karyotypes remain the only reliable, diagnostic criterion for identification of individuals in areas of Kansas, Iowa, and Missouri where *hylophaga* and *kirtlandi*-sized *brevicauda* occur in sympatry. Comparison of skulls of karyotyped individuals from Douglas County, Kansas, and Platte County, Missouri, with those of *hylophaga* from western Kansas and topotypical *kirtlandi* substantiated the situation described by Graham and Semken (1976)—individuals at the extremes of mensural variation of the two taxa are exceedingly difficult to identify. Additional karyologic and morphometric studies of short-tailed shrews from areas of sympatry are needed to resolve problems in identification of specimens of *B. brevicauda* and *B. hylophaga* in those regions.

In marked contrast to the geographic relationships found between *brevicauda* and *carolinensis* [= *hylophaga*] in Nebraska by Jones (1964) and Genoways and Choate (1972), there is no sharply-defined line of contact between those taxa in Iowa and Missouri. Data presented herein support the contention by Bowles (1975:34) that "Specimens easily referable to one or the other [taxon] have been taken at sites varying from 25 to 50 miles apart along the zone of contact"

The known distribution of *Blarina hylophaga* in Missouri and Iowa extends northward to Fremont, Page, Taylor, Marion, and Keokuk counties, Iowa, whereas the known distribution of *B. brevicauda* includes all of Iowa and extends southward in Missouri to Platte, Randolph, and Ralls counties (Fig. 3). The two species occur sympatrically in a broad zone across southern Iowa and northern Missouri. In Kansas, *kirtlandi*-sized shrews assigned to *brevicauda* occur in at least Douglas and Miami counties, whereas *hylophaga* occurs throughout the state. Another species of short-tailed shrew, *B. carolinensis*, occurs in the "bootheel" region of Missouri and might be sympatric with *B. hylophaga* on the floodplain of the Mississippi River (George et al., 1981).

SPECIMENS EXAMINED

Asterisks denote localities at which specimens assigned to both *Blarina brevicauda* and *B. hylophaga* were collected.

Blarina brevicauda

ILLINOIS. *Champaign Co.*: 2½ mi. NE Urbana, 4 (1 KU, 3 UCM); 1 mi. N, 2 mi. E Urbana, 1 (KU). *McLean Co.*: Bloomington, 6 (UMMZ).

IOWA. *Adams Co.*: 4 mi. N, ¾ mi. W Nodaway, 1 (KU). *Chickasaw Co.*: 1 mi. S, 1 mi. W North Washington, 10 (KU). *Decatur Co.*: 1 mi. (by road) N Davis City, 1 (CM); 4½ mi. (by road) NW Pleasanton, 6 (3 CM, 3 MHP); 3 mi. (by road) NW Pleasanton, 2 (1 CM, 1 MHP); ¾ mi. N, ¼ mi. E Woodland, 1 (KU). *Fremont Co.*: 2 mi. S, 3 mi.

E Tabor*, 3 (1 CM, 2 MHP); 2 mi. S, 4 mi. E Tabor, 4 (3 CM, 1 MHP). *Guthrie Co.*: Springbrook State Park, 2 (ROM). *Henry Co.*: Hillsboro, 2 (USNM). *Howard Co.*: T.98N, R.11W, sec. 1, 2 (CUI); T.98N, R.11W, sec. 2, 5 (CUI). *Keokuk Co.*: Sigourney, 3 (KU); 6½ mi. S, 1 mi. W Sigourney*, 1 (KU). *Lucas Co.*: 2½ mi. S, 2½ mi. E Chariton, 1 (CUI); 2½ mi. N, 2½ mi. E Russell, 1 (KU); 1 mi. N, 2½ mi. E Russell, 1 (KU). *Mahaska Co.*: 5½ mi. N Oskaloosa, 2 (KU); 5 mi. N Oskaloosa, 1 (KU); 2 mi. N, 2½ mi. E Oskaloosa, 1 (KU); 2 mi. N, 3 mi. E Oskaloosa, 1 (KU); 1 mi. W Oskaloosa, 1 (KU); Oskaloosa, 2 (KU); 5 mi. E Oskaloosa, 1 (KU); 2 mi. S, 10 mi. W Oskaloosa, 1 (KU); 2½ mi. S, 4 mi. W Oskaloosa, 2 (KU); 3 mi. S, 9 mi. W Oskaloosa, 1 (KU); 3½ mi. SW Oskaloosa, 2 (KU); 5 mi. E Penn College, 1 (KU). *Marion Co.*: 1¼ mi. N, 2¼ mi. W Bussey, 2 (KU); 5¾ mi. N Knoxville, 1 (KU); 4½ mi. N Knoxville, 4 (KU); Knoxville, 2 (USNM); 5½ mi. N, 3 mi. W Pella, 3 (CUI); 1 mi. S, 3 mi. W Pella, 2 (CUI); 1 mi. S Pella, 1 (CUI); 1½ mi. S, ¼ mi. W Pella*, 50 (CUI); 1½ mi. S Pella, 1 (CUI); 2½ mi. S, 2½ mi. W Pella, 1 (CUI); 2½ mi. S, 1½ mi. E Pella, 1 (CUI); ½ mi. W Tracy, 1 (KU). *Mills Co.*: ½ mi. S, 3 mi. W Henderson, 7 (KU); 3 mi. S, 2½ mi. W Hillsdale, 1 (CUI); 3½ mi. N, 2 mi. E Tabor (in Fremont Co.), 7 (3 CM, 4 MHP); 2 mi. N, ½ mi. E Tabor (in Fremont Co.), 1 (CM); 2 mi. N, 1½ mi. E Tabor (in Fremont Co.), 1 (CM). *Monroe Co.*: 5½ mi. N, 3½ mi. E Albia, 1 (KU); 1 mi. N, 2 mi. E Albia, 1 (CUI); 5 mi. S Albia, 3 (CUI); 1½ mi. N Melrose, 2 (KU). *Montgomery Co.*: 1½ mi. S, 2 mi. E Wales, 4 (KU). *Page Co.*: 1 mi. W Bethesda, 1 (MHP); 1 mi. N, 2 mi. E Imogene (in Fremont Co.)*, 1 (MHP); 1 mi. N, 6 mi. E Imogene (in Fremont Co.)*, 1 (CM). *Polk Co.*: Des Moines, 1 (USNM). *Pottawattamie Co.*: Council Bluffs, 7 (USNM). *Poweshiek Co.*: 1 mi. S, 2 mi. W Grinnell, 1 (KU). *Ringgold Co.*: 2 mi. N Blockton (in Taylor Co.), 3 (1 CM, 2 MHP); 1 mi. S Blockton (in Taylor Co.), 3 (1 CM, 2 MHP); 3 mi. S Blockton (in Taylor Co.), 1 (CM); ½ mi. N, 2 mi. E Mt. Ayr, 3 (KU). *Taylor Co.*: ½ mi. S, 1 mi. E Lenox, 3 (2 CM, 1 MHP); 2 mi. S, 1 mi. E Lenox, 1 (CM); 4½ mi. S, 1 mi. E Lenox, 2 (1 CM, 1 MHP); 5 mi. S, 1 mi. E Lenox, 1 (CM); 6 mi. S, 1 mi. E Lenox, 4 (2 CM, 2 MHP); 10 mi. S Lenox*, 2 (1 CM, 1 MHP); 12 mi. S Lenox, 16 (8 CM, 8 MHP); 14 mi. S Lenox, 2 (1 CM, 1 MHP); 17 mi. S, 1 mi. E Lenox*, 2 (1 CM, 1 MHP); 19 mi. S, 1 mi. E Lenox, 3 (1 CM, 2 MHP). *Union Co.*: 1¾ mi. N, ½ mi. E Thayer, 4 (KU). *Winnesheik Co.*: Conover, 3 (UMMZ); Decorah, 7 (3 SHMC, 4 UMMZ); Ridgeway, 1 (UMMZ).

KANSAS. *Douglas Co.*: 2½ mi. N, ½ mi. E Lawrence (T.12S, R.20E, W ½ sec. 20), 2 (MHP); 2 mi. N, 1⅔ mi. E Lawrence, (T.12S, R.20E, SE ¼ sec. 20), 2 (MHP); 1½ mi. N, 1⅓ mi. E Lawrence*, 1 (KU); Lawrence*, 1 (KU); 7½ mi. SW Lawrence*, 1 (KU). *Miami Co.*: 11 mi. SSE Paola*, 1 (KU).

MISSOURI. *Adair Co.*: ½ mi. (by road) W Brashear*, 5 (2 CM, 3 MHP); 3 mi. N Connelville, 1 (CM). *Buchanan Co.*: St. Joseph, 1 (MOU). *Clark Co.*: 1½ mi. N, 3 mi. W Antioch (T.64N, R.8W, NW ¼ sec. 14)*, 1 (MHP). *Grundy Co.*: 3½ mi. (by road) S Modena (in Mercer Co.)*, 1 (CM); 6½ mi. (by road) S Modena (in Mercer Co.)*, 7 (2 CM, 5 MHP); 2½ mi. S Tindall*, 5 (2 CM, 3 MHP). *Lewis Co.*: 1½ mi. N Canton (T.62N, R.5W, SE ¼ sec. 23), 1 (CM); ½ mi. S, 2½ mi. E Deer Ridge (T.62N, R.9W, E ½ sec. 2)*, 1 (CM); ½ mi. S, 3 mi. E Deer Ridge (T.62N, R.9W, E ½ sec. 1), 1 (MHP); 2 mi. S, 2 mi. E Deer Ridge (T.62N, R.9W, SE ¼ sec. 11), 1 (CM); 2½ mi. S, 2 mi. E Deer Ridge (T.62N, R.9W, E ½ sec. 14), 1 (MHP). *Mercer Co.*: 14½ mi. (by road) N Goshen, 4 (2 CM, 2 MHP); 11 mi. (by road) N Goshen, 1 (MHP); 9 mi. (by road) N Goshen, 1 (MHP); 3 mi. (by road) N Goshen, 1 (CM); 1 mi. (by road) N Goshen*, 4 (2 CM, 2 MHP); 1½ mi. (by road) S Goshen, 1 (MHP); 5½ mi. (by road) S Goshen, 1 (MHP). *Platte Co.*: ¼ mi. N, 1 mi. W Weston (T.53N, R.36W, NW ¼ sec. 10), 1 (MHP). *Ralls Co.*: Hannibal, 1 (MOU). *Randolph Co.*: Moberly, 1 (MOU).

NEBRASKA. *Boyd Co.*: 5 mi. WNW Spencer, 1 (KU). *Burt Co.*: 1 mi. E Tekamah, 1 (KU). *Butler Co.*: 4 mi. E Rising City, 1 (KU). *Cedar Co.*: 4 mi. SE Laurel, 6 (KU). *Cherry Co.*: 3 mi. SSE Valentine, 1 (KU). *Holt Co.*: 1 mi. S Atkinson, 1 (KU); 6 mi.

N Midway, 1 (KU). *Knox Co.*: 3 mi. W Niobrara, 1 (KU). *Washington Co.*: 6 mi. SE Blair, 4 (KU). *Wayne Co.*: ½ mi. W Wayne, 3 (KU); Wayne, 5 (KU).

OHIO. *Ashtabula Co.*: Farnham, 2 (CMNH); Mechanicsville, 7 (KU). *Geauga Co.*: Chesterland Caves, 19 (CMNH); Holden Arboretum, 1 (KU). *Lake Co.*: Holden Arboretum, 3 (KU).

Blarina hylophaga

IOWA. *Fremont Co.*: 6 mi. N, 3 mi. W Hamburg, 2 (KU); 4 mi. E Hamburg, 9 (KU); 13 mi. E Hamburg, 18 (KU); 1 mi. S Hamburg, 3 (KU); 3 mi. S, 1 mi. E Imogene, 1 (CUI); ½ mi. N, 1 mi. W Riverton, 4 (CUI); 3½ mi. S Sidney, 5 (KU); 4 mi. S, 9 mi. W Sidney, 2 (KU); 5 mi. S, 2 mi. W Sidney, 7 (KU); 2 mi. S, 3 mi. E Tabor*, 2 (1 CM, 1 MHP); 2½ mi. S, 6 mi. E Tabor, 4 (2 CM, 2 MHP); 2½ mi. S, 11 mi. E Tabor, 1 (MHP). *Keokuk Co.*: 6½ mi. S, 1 mi. W Sigourney*, 1 (KU). *Marion Co.*: 1½ mi. S, ¼ mi. W Pella*, 1 (CUI). *Page Co.*: 7 mi. W Bethesda, 1 (CM); 3½ mi. W Bethesda, 2 (1 CM, 1 MHP); 7/10 mi. S Coin, 3 (KU); 1 mi. N, 2 mi. E Imogene (*in Fremont Co.*)*, 4 (3 CM, 1 MHP); 1 mi. N, 4½ mi. E Imogene (*in Fremont Co.*), 1 (MHP); 1 mi. N, 6 mi. E Imogene (*in Fremont Co.*)*, 2 (MHP); 1 mi. N, 7½ mi. E Imogene (*in Fremont Co.*), 2 (1 CM, 1 MHP); 1 mi. S, 3 mi. E Northboro, 4 (KU); 2 mi. S, ½ mi. W Shambaugh, 1 (KU). *Taylor Co.*: 2 mi. S, ¾ mi. W Bedford, 1 (KU); 1 mi. S, 1 mi. E Lenox, 1 (MHP); 10 mi. S Lenox*, 1 (CM); 17 mi. S, 1 mi. E Lenox*, 1 (CM).

KANSAS. *Allen Co.*: Moran, 3 (KU); no locality specified, 1 (KU). *Anderson Co.*: 7 mi. S Garnett, 1 (KU); 1 mi. N Welda, 1 (KU). *Archison Co.*: 18/10 mi. N Atchison, 1 (KU); 1½ mi. S Muscotah, 7 (KU). *Brown Co.*: Brown County State Lake, 1 (MHP); 7 mi. N, ½ mi. E Hiawatha, 1 (KU); 3 mi. N Hiawatha, 1 (KU); 1 mi. S, 7 mi. E Hiawatha, 1 (MHP); 5 mi. S Hiawatha, 1 (KU); 1 mi. N Horton, 1 (KU). *Butler Co.*: 2 mi. N, 3/10 mi. W El Dorado, 1 (MHP). *Chase Co.*: 9 mi. E Lincolnville, 1 (KU); ¼ mi. N Matfield Green, 1 (KU). *Chautauqua Co.*: 1 mi. W Wauneta, 1 (KU). *Cherokee Co.*: 1½ mi. S Galena, 1 (KU); 1 mi. N Tri-State Monument, 1 (KU); no locality specified, 1 (KU). *Coffey Co.*: 2½ mi. S Burlington, 2 (KU). *Cowley Co.*: 6 mi. N, 12 mi. E Arkansas City, 1 (KU); 8/10 mi. E Arkansas City, 2 (KU); 3 mi. SE Arkansas City, 4 (KU); 2 mi. N, 3 mi. E Cameron City (T.34S, R.6E, S ½ sec. 8), 1 (MHP); 2 mi. S, ½ mi. W Udall, 1 (KU). *Crawford Co.*: 2 mi. N, 1 mi. E Arma, 1 (KSCP); 1 mi. N, 2 mi. E Cherokee, 1 (KSCP); 1¼ mi. E Crawford County State Lake, 1 (KSCP); Pittsburg, 5 (4 KSCP, 1 UWSP); 2½ mi. E Pittsburg, 1 (KSCP); 2½ mi. SW Pittsburg, 1 (KSCP); 5 mi. S, 1 mi. W Pittsburg, 1 (KSCP). *Dickinson Co.*: ½ mi. S Chapman (T.12S, R.4E, sec. 32), 1 (MHP); 2 mi. W Herington, 6 (MHP). *Doniphan Co.*: Geary, 1 (KU); ½ mi. N, ½ mi. W Severance, 1 (KU). *Douglas Co.*: 1¼ mi. N Baldwin City, 1 (KU); ½ mi. S, 5/10 mi. W Clinton, 1 (KU); ½ mi. W Eudora, 2 (KU); 7 mi. NNE Lawrence, 2 (KU); 6 mi. NNE Lawrence, 1 (KU); 5 mi. N Lawrence, 2 (KU); 48/10 mi. N, 7/10 mi. E Lawrence (T.12S, R.20E, sec. 5), 1 (KU); 22/10 mi. N, 8/10 mi. E Lawrence, 2 (KU); 2 mi. N Lawrence, 1 (KU); 2 mi. N, 2 mi. E Lawrence, 2 (KU); 1½ mi. N, 1¾ mi. E Lawrence, 7 (3 KU, 4 MHP); 1½ mi. N, 1½ mi. E Lawrence*, 11 (KU); 1 mi. N, 4 mi. W Lawrence, 1 (KU); ½ mi. N, 1 mi. E Lawrence, 1 (KU); 2½ mi. W Lawrence, 1 (KU); 1 mi. W Lawrence, 4 (KU); Lawrence*, 14 (KU); 8/10 mi. S, 2½ mi. W Lawrence, 1 (KU); 39/10 mi. S, 29/10 mi. E Lawrence, 1 (KU); 5¾ mi. S, ¾ mi. W Lawrence, 1 (KU); 7 mi. SW Lawrence, 4 (KU); 7½ mi. SW Lawrence*, 2 (KU); ½ mi. S, ½ mi. E Pleasant Grove, 1 (KU); Rock Creek, 1 (KU); 1 mi. S, 1¼ mi. W Vinland, 1 (KU); no locality specified, 13 (KU). *Ellis Co.*: 1 mi. S, 6½ mi. W Antonino (T.15S, R.20W, sec. 2), 5 (MHP); Ellis, 1 (MHP); 16 mi. N, 1 mi. W Hays, 2 (MHP); 9 mi. N, 4 mi. W Hays (T.12S, R.19W, NE ¼ sec. 14), 2 (MHP); 8½ mi. N, 4 mi. W Hays (T.12S, R.19W, SE ¼ sec. 14), 1 (MHP); Hays (T.14S, R.18W, sec. 4), 1 (MHP); 2½ mi. SW Hays, 1 (MHP). *Geary Co.*: 5 mi. S Grandview Plaza (T.12S, R.5E, NE ¼ sec. 25), 1 (MHP).

Greenwood Co.: Hamilton, 30 (2 CM, 22 KU, 1 MMNH, 5 UMMZ); ½ mi. E Hamilton, 2 (KU); ¼ mi. S Hamilton, 2 (KU); ¼ mi. SE Hamilton, 1 (KU); ½ mi. S Hamilton, 5 (KU); ½ mi. SE Hamilton, 1 (KU); ¾ mi. S Hamilton, 1 (KU); 1 mi. S Hamilton, 2 (KU); 1½ mi. S Hamilton, 4 (KU); 8½ mi. SW Toronto (in Woodson Co.), 1 (KU). *Jackson Co.*: Holton, 1 (KU); 5½ mi. E Holton, 2 (KU). *Jefferson Co.*: 5 mi. N, 2 mi. E Lawrence (in Douglas Co.), 1 (KU); 4 mi. N, 2 mi. E Lawrence (in Douglas Co.), 1 (KU). *Labette Co.*: 2 mi. SW Parsons, 1 (KU); 3 mi. S, 2 mi. E Parsons, 1 (KSCP). *Leavenworth Co.*: 1 mi. N, 4 mi. W Bonner Springs (in Wyandotte Co.), 2 (KU); no locality specified, 1 (KU). *Linn Co.*: ½ mi. N, 4 mi. W Prescott, 1 (KU). *Lyon Co.*: Emporia, 1 (UMMZ). *Marion Co.*: 1 mi. N, ½ mi. E Lincolnville, 1 (KU). *Marshall Co.*: 2 mi. N, ½ mi. E Oketo, 5 (MHP); 1½ mi. N, ½ mi. W Oketo (T.1S, R.7E, NW ¼ sec. 11), 1 (MHP); 1½ mi. N Oketo, 2 (MHP); 1 mi. N Oketo, 3 (MHP); 1 mi. W Oketo, 1 (MHP); Lake Idlewild, 1½ mi. N, ½ mi. E Waterville, 1 (KU); 1 mi. N Waterville, 1 (KU); ½ mi. NW Waterville, 1 (KU); 1 mi. E Waterville, 4 (KU); ½ mi. SW Waterville, 2 (KU). *Miami Co.*: 11 mi. SSE Paola*, 1 (KU). *Montgomery Co.*: Coffeyville, 1 (OU); Independence, 1 (KU). *Morris Co.*: 4½ mi. S, 5½ mi. W Council Grove, 1 (KU). *Nemaha Co.*: 6 mi. N Sabetha, 1 (KU); 2½ mi. S Sabetha, 2 (KU); 3½ mi. S, ¾ mi. E Sabetha, 3 (KU). *Osage Co.*: 1¾ mi. S, 1⁷/₁₀ mi. E Berryton, 1 (KU); 8 mi. N, 9 mi. E Osage City, 10 (MHP); 1 mi. S, 4 mi. E Scranton (T.15S, R.16E, NE ¼ sec. 7), 3 (MHP). *Osborne Co.*: T.9S, R.12W, NE ¼ sec. 30, 1 (MHP). *Phillips Co.*: 1 mi. S, 1 mi. W Agra, 1 (MHP); ¾ mi. S, ¼ mi. W Kirwin (T.4S, R.16W, NE ¼ sec. 33), 1 (MHP); 1 mi. S Kirwin, 1 (MHP); 3¾ mi. S, 3 mi. W Kirwin (T.5S, R.17W, E ½ sec. 13), 2 (MHP); 4½ mi. S, 3¼ mi. W Kirwin (T.5S, R.17W, NE ¼ sec. 4), 1 (MHP); 5 mi. S, 4 mi. W Kirwin (T.5S, R.17W, SE ¼ sec. 23), 1 (MHP). *Pottawatomie Co.*: Manhattan, 2 (USNM); Onaga, 2 (USNM); 5 mi. N Westmoreland, 2 (MHP). *Riley Co.*: Fort Riley, 1 (USNM); Manhattan, 2 (1 KU, 1 UMMZ). *Rooks Co.*: 3 mi. S, 3 mi. W Stockton, 1 (MHP). *Rush Co.*: 1¹/₁₆ mi. E LaCrosse (T.17S, R.18W, S ½ sec. 34), 1 (MHP). *Russell Co.*: 5 mi. N, 1 mi. E Dorrance (T.13S, R.11W, NE ¼ sec. 17), 1 (MHP); 8½ mi. S, ½ mi. E Lucas (T.13S, R.11W, NE ¼ sec. 10), 1 (MHP). *Shawnee Co.*: 1 mi. N, 3 mi. W Auburn, 5 (KU); 4½ mi. N, 3 mi. W Topeka, 1 (KU); 1⁹/₁₀ mi. N, 1 mi. E Wakarusa, 1 (KU). *Trego Co.*: ½ mi. N, 3 mi. W Ellis (in Ellis Co.) (T.13S, R.21W, NE ¼ sec. 11), 1 (MHP). *Woodson Co.*: Neosho Falls, 3 (2 KU, 1 USNM); 2½ mi. N Toronto, 1 (KU); 2 mi. S Toronto, 1 (KU).

MISSOURI. *Adair Co.*: ½ mi. (by road) W Brashear*, 2 (CM). *Andrew Co.*: Amazonia, 1 (MOU); St. Joseph, 3 (MOU). *Barry Co.*: no locality specified, 1 (MOU). *Boone Co.*: Ashland, 1 (MOU); Hinkson Creek, 2 (MOU); Columbia, 25 (MOU); McBaine, 3 (MOU); no locality specified, 6 (MOU). *Callaway Co.*: Alles, 1 (MOU). *Camden Co.*: Hahatonka, 2 (UMMZ). *Chariton Co.*: Forest Green, 1 (MOU). *Clark Co.*: 1½ mi. N, 3 mi. W Antioch (T.64N, R.8W, NW ¼ sec. 14)*, 1 (CM). *Douglas Co.*: T.27N, R.13W, sec. 1, 1 (MOU). *Franklin Co.*: Meramec State Park, 2 (MOU); Washington, 1 (MOU). *Gentry Co.*: King City, 1 (MOU). *Greene Co.*: Springfield, 4 (MOU). *Grundy Co.*: 3½ mi. (by road) S Modena (in Mercer Co.)*, 1 (MHP); 5 mi. (by road) S Modena (in Mercer Co.), 1 (MHP); 6½ mi. (by road) S Modena (in Mercer Co.)*, 2 (CM); 2½ mi. S Tindall*, 1 (CM). *Holt Co.*: ½ mi. N Fortescue (T.61N, R.39W, W ½ sec. 32), 8 (4 CM, 4 MHP); Mound City, 1 (MOU). *Jackson Co.*: Independence, 1 (USNM); Kansas City (56th and Swope Parkway), 1 (KU); Kansas City, 2 (MOU); T.48N, R.32W, sec. 22, 1 (MOU); no locality specified, 2 (MOU). *Jefferson Co.*: Kimswick, 1 (USNM). *Johnson Co.*: Warrensburg, 1 (MOU). *Lewis Co.*: ½ mi. S, 2½ mi. E Deer Ridge (T.62N, R.9W, E ½ sec. 2)*, 1 (MHP); 2½ mi. S, 3 mi. E Deer Ridge (T.62N, R.9W, E ½ sec. 13), 1 (CM). *Lincoln Co.*: ½ mi. S, 2½ mi. W (by road) Foley, 1 (CM); 1½ mi. N Winfield, 2 (1 CM, 1 MHP). *McDonald Co.*: ½ mi. N, 4 mi. E Noel, 1 (KU). *Mercer Co.*: 1 mi. (by road) N Goshen*, 2 (1 CM, 1 MHP). *Morgan Co.*: Gravois Mills, 1 (MOU). *Nodaway Co.*: Burlington Junction, 1 (MOU). *Pettis Co.*: T.44N, R.21W, sec.

3, 1 (KU). *Ray Co.*: no locality specified, 1 (MOU). *Saline Co.*: 4 mi. (by road) W Glasgow (in Howard Co.), 1 (CM); no locality specified, 2 (MOU). *St. Clair Co.*: no locality specified, 1 (MOU). *Wright Co.*: Mountain Grove, 1 (MOU).

OKLAHOMA. *Cleveland Co.*: Norman, 2 (1 KU, 1 OU); 2 mi. S, 1 mi. W Norman, 1 (OSU); 4 mi. S Norman, 1 (OU); 5 mi. S Norman, 1 (OU). *Garvin Co.*: 3 mi. N, 2 mi. W (by road) Davis (in Murray Co.), 1 (MHP). *McClain Co.*: 8 mi. W Norman (in Cleveland Co.), 1 (KSCP). *Murray Co.*: Platt National Park, 5 (KU); $1\frac{3}{10}$ mi. S, $2\frac{2}{10}$ mi. W (by road) Davis, 4 (MHP); $5\frac{7}{10}$ mi. S, $2\frac{3}{10}$ mi. W (by road) Davis, 1 (MHP). *Payne Co.*: Lake Carl Blackwell, 9 mi. W Stillwater, 1 (OSU); Lake Carl Blackwell, 7 mi. W Stillwater, 1 (OSU); 6 mi. W Stillwater, 1 (OSU); 3 mi. W Stillwater, 2 (OSU); Stillwater, 1 (OSU); 2 mi. S, $\frac{1}{2}$ mi. E Stillwater, 1 (OSU); $2\frac{1}{2}$ mi. S Stillwater, 2 (OSU); T.18N, R.2E, sec. 2, 1 (OSU); no locality specified, 1 (OSU).

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APPENDIX 1

Counties included within samples 1-22 (with sample sizes indicated in parentheses) were as follows: 1) Iowa—Fremont, Guthrie, Mills, Montgomery, Page, and Pottawatomie (30); 2) Iowa—Adams, Decatur, Ringgold, Taylor, and Union (56); 3) Iowa—Keokuk, Lucas, Mahaska, Marion, Monroe, and Poweshiek (62); 4) Missouri—Grundy and Mercer (20); 5) Missouri—Adair, Clark, and Lewis (10); 6) Kansas—Douglas and Miami, and Missouri—Buchanan (5); 7) Iowa—Fremont (47); 8) Iowa—Page and Taylor (21); 9) Iowa—Keokuk and Marion, and Missouri—Adair, Clark, Grundy, Lewis, and Mercer (11); 10) Kansas—Geary, Marshall, Nemaha, Pottawatomie, and Riley (20); 11) Kansas—Atchison, Brown, and Doniphan (13); 12) Kansas—Leavenworth, and Missouri—Andrew, Gentry, Holt, Jackson, and Ray (19); 13) Kansas—Dickinson, Marion, and Morris (7); 14) Kansas—Jackson, Jefferson, and Shawnee (10); 15) Kansas—Chase, Greenwood, and Lyon (27); 16) Kansas—Anderson, Coffey, and Osage (11); 17) Kansas—Douglas and Miami (54); 18) Kansas—Butler, Chautauqua, and Cowley (8); 19) Kansas—Allen, Cherokee, Crawford, Labette, and Woodson, and Missouri—McDonald (12); 20) Missouri—Camden, Greene, Morgan, Pettis, and Wright (7); 21) Missouri—Boone (23); 22) Missouri—Franklin and Lincoln (6).

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BLAWNOX: AN UPPER OHIO VALLEY MIDDLE WOODLAND SITE

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ABSTRACT

The now largely destroyed Blawnox Site, 36AL19, located on a lower Allegheny River floodplain, was test excavated by Carnegie Museum of Natural History in 1979-1980. A deep Middle Woodland component allowed an analysis of chert utilization and chipped stone tool typology within a restricted temporal framework. The data suggest that, with the termination of the Hopewell Interaction Sphere, Upper Ohio Valley populations were participants in a region-wide technological shift that was here manifested by the emergence of several projectile point types and a greater reliance on locally available lithic materials.

INTRODUCTION

A proposed construction project at the Blawnox Site, 36AL19 (Fig. 1), provided archaeologists from Carnegie Museum of Natural History with an opportunity to examine several aspects of Middle Woodland occupation in the Upper Ohio Valley. A flood plain on the north bank of the Allegheny River in Allegheny County, Pennsylvania, was to be the location of a recreational facility to be constructed by Ross Real Estate, Pittsburgh, and the Museum was contracted to evaluate the cultural resources of the site. Funding was provided by Joseph Ross and he is thanked for his encouragement and considerations.

SITE HISTORY

The Blawnox Site (Fig. 2) was recorded as 36AL19 in 1952 by William J. Mayer-Oakes during the Upper Ohio Valley Archaeological Survey. The site was shown to Mayer-Oakes by W. C. Reeves who

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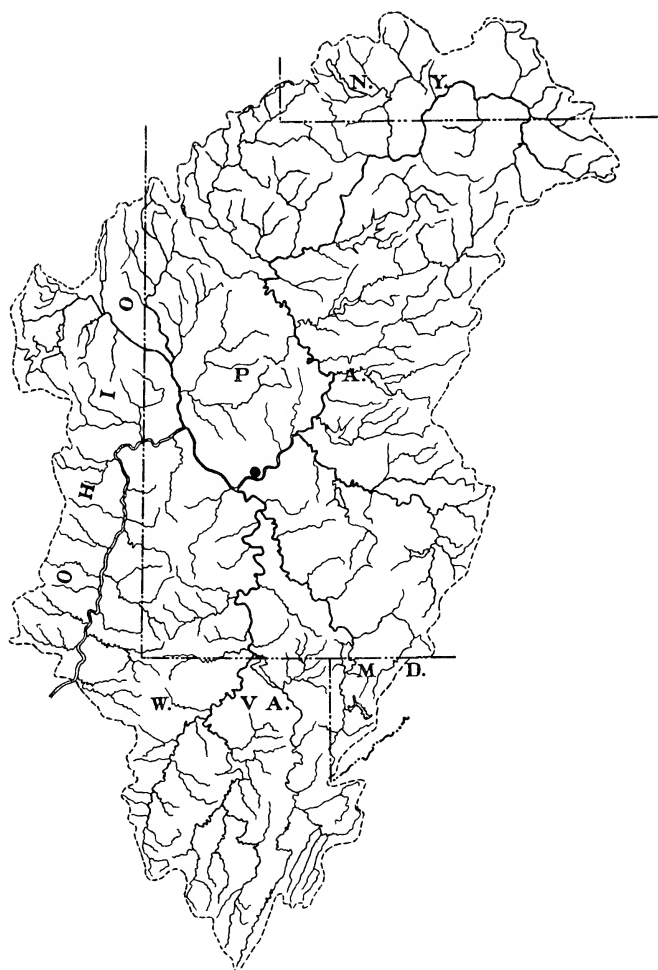


Fig. 1.—Location of the Blawnox site, 36 AL 19.

subsequently was employed as a part-time Laboratory Assistant at Carnegie Museum of Natural History. When recorded, the site was partially under cultivation by the Allegheny County Workhouse. A former warden of this prison facility, Colonel Edward R. Ayres, had collected artifacts from the site's cultivated fields around 1900 and these were donated to the Museum in 1971 by Mrs. Ayres. From this collection representative artifacts from Paleoindian through the Contact period were noted from this large flood plain and adjacent beach.

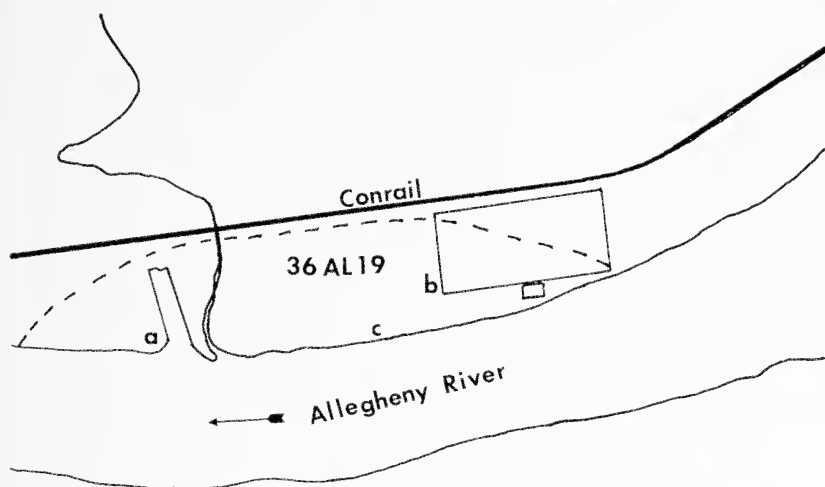


Fig. 2.—Blawnox Site locational details: a) Area of Stein excavation; b) Papercraft Corporation plant and parking lot; c) Carnegie Museum of Natural History's 1979–80 excavation area.

The long temporal span of the Blawnox Site was also reflected by surface collected artifacts donated to the Museum by W. C. Reeves, H. L. Beals, and the author. Included were numerous items of Middle Woodland origin.

From 1956 through 1958, Walter T. Stein conducted intermittent excavations immediately down-river from an artificial inlet near the mouth of Squaw Run (Fig. 2a). In an unpublished paper on file at the Museum, Stein reported the presence of a Late Woodland Monongahela component that was recognized in 15 excavation units (Stein, 1959:5–7). He recorded no postmolds nor burials but did uncover four features in an area disturbed by heavy machinery prior to 1956. Artifacts included 1085 shell tempered sherds, 30 of which were rims; ceramic pipe fragments; 16 triangular points and fragments; a sandstone celt; an unfinished platform pipe of stone and a perforated slate pendant or gorget fragment. Bone refuse, mussel shells, and charred nut hull fragments were also recorded. Stein (1959:11) concluded that the area excavated was a Monongahela village refuse dump based on the absence of postmolds and burials. A recent visit to the locale of Stein's work indicated extreme land disturbance leaving little doubt that this portion of the site, affected by industrialization, is now destroyed.

From 1959 until 1965, the author made periodic reconnaissances of

the site. During the latter year, a large portion of the flood plain and site was destroyed by the construction of a paper processing plant owned by Papercraft Corporation (Fig. 2b). Approximately 20,000 square m of land was redistributed for construction of the plant, an office building and parking lot. Subsoil exposed by the stripping of topsoil revealed no features nor areas of artifact concentrations except for a cache of 17 blades, blanks, quarry blocks, and flakes. The majority of the items were of banded gray quarry chert of unknown origin. One blank was of fossiliferous chert that may have been thermally altered based on the surface gloss.

After 1965, the only area open for surface surveillance was the river beach immediately down river from the Papercraft Corporation parking lot. Margaret and Vernon Adams of the Allegheny Chapter #1, Society for Pennsylvania Archaeology, made frequent visits to the beach and it was in this area where the excavations were carried out in 1979–1980 (Fig. 2c). Second growth timber, berry bushes, shrubs, and grassy glens characterized the extant flora.

Topography

The Blawnox site occupied a typical post-Wisconsin flood plain (Fig. 2) in the lower Allegheny River valley. With the retreat of the Wisconsin glacier and a decrease in volume of water and sediments, the river cut new channels, and locally reworked the Wisconsin valley-fill. The results are low terraces, including the modern flood plain, about 10 to 30 ft above present river level (Heyman, 1970:92). The existing flood plain in the area of the excavation was approximately 3 m above summer pool stage. The installation of a lock and dam system for navigation on the Allegheny River by the U.S. Army Corps of Engineers, beginning in 1898, had resulted in continuing bank erosion and flood plain site destruction. During the 21 years that the author had periodically visited the site, observable, though not measured, bank erosion had taken place in areas not protected by vegetation. The river here is now approximately 300 m wide and the flood plain is narrower than before 1898. The quantity of artifacts found on the river beach by the author and others attest to the continuing bank erosion.

From 15 to 30 m to the north of the present bank, a second terrace with an elevation only 1.5 m higher is located. Further to the north, and 150 m from the bank, the land undulates with low relief ridges and hillocks among marshy zones. Although appearing natural, this topography could have resulted from the building of the Pennsylvania Main Line Canal between 1826 and 1830 (Lewba and McCullough, 1960). Now covered by the right-of-way of Conrail (Fig. 2), the canal, 1.2 m deep and 8.3 m wide at the bottom, operated from its date of completion until 1867 when railroads began to dominate surface transporta-

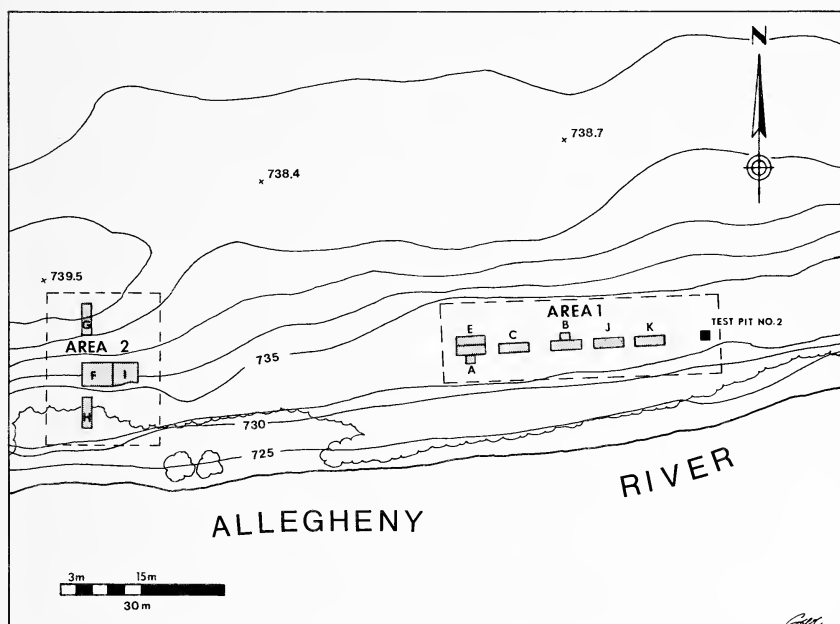


Fig. 3.—Location of excavation units in Areas 1 and 2.

tion. It is probable that much of the flood plain immediately south of the Conrail tracks was affected by canal and railroad construction and operation. Prehistoric occupational evidence in this area could thus have been severely disturbed if not destroyed before 1900.

EXCAVATION METHODOLOGY

Thirty shovel tests were made over the area to be impacted by construction. Testing on the second terrace and in the area of undulating terrain, in the north and northwest, indicated that artifacts were limited to the disturbed topsoil although most areas were sterile. The level land adjacent to the river bank was found to have stratigraphic integrity. After testing with 1 m square units, 10 trenches were hand excavated to various depths. All were 2 m by 5 or 6 m and were confined to areas 1 and 2 (Fig. 3). It was within Area 1, where six trenches were dug, that a deep Middle Woodland occupation zone was encountered. Four of the six trenches, Units B, C, J, and K, were excavated to depths of 1 m or deeper. Table 1 shows the horizontal dimensions and depths of Area 1 excavation units.

AREA 1

Recently deposited brown sandy loam occurred to a depth of at least 25 cm in all Area 1 units (Fig. 4). Only near the bottom of this zone were prehistoric and historic artifacts found. Between 25 and 50 cm,

Table 1.—*Horizontal dimensions and depths of Area 1 excavation units.*

Unit	Horizontal dimension	Maximum excavated depth
A	5 × 2 M	50 cm
B	6 × 2 M	120 cm
C	6 × 2 M	130 cm
E	5 × 2 M	50 cm
J	5 × 2 M	150 cm
K	5 × 2 M	100 cm

an old plow zone was characterized by soil mixing, undulation, and sandy deposits. A photograph of the floodplain taken in 1930 showed the area of excavation as a cultivated field. Plow disturbance would explain the historic-prehistoric mix of artifacts recorded in this zone. No historic materials were found below 50 cm where dark brown loam continued to the maximum excavated levels. There was an increase in compactness as the units were deepened and a subtle lightening of soil color.

Four 2 m wide units were also excavated in Area 2 located downriver from Area 1. Units F and G were 6 m long and excavated to a depth of 25 and 20 cm respectively. Both Unit H and I were 5 m long and excavated to a depth of 21 and 25 cm respectively. A few diagnostic Middle Woodland artifacts and six Late Woodland triangular points were found in Area 2 and will be described later.

Area 1 Features

Nine features were recorded in Area 1 and their characteristics are shown on Table 2. The most numerous of features, stone hearths, consisted of clusters of fire burnt pebbles and associated charcoal flecks without recognizable soil staining. They all appeared to be the remains of Middle Woodland surface hearths that had been subsequently subjected to the deprivations of weather based on the paucity of charcoal and staining. Some of the stone hearth pebbles had battered surfaces indicating use as hammerstones. Of 17 whole and fragmented pebbles of Feature 11, three had functioned as hammerstones. A utilized pebble core fragment was found in Feature 11. It was the only chipped stone tool found in a stone hearth.

Feature 5 was a hearth with an 18 cm deep mix of fire burnt soil and charcoal. Surrounding it were scattered charcoal flecks, fragments of fire burnt stone, and several chert flakes. Feature 6 consisted of a dark lens containing charcoal, fire burnt stone fragments, and one chert flake.

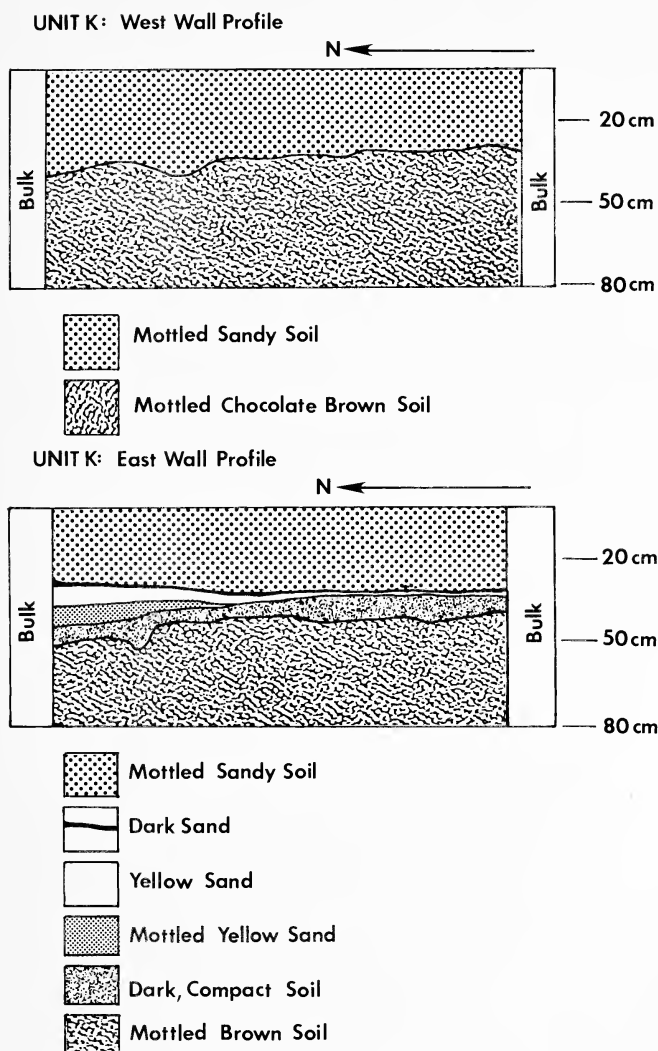


Fig. 4.—Soil profile of Unit K, East and West Walls.

Features other than hearths were rare. A single postmold, Feature 1, was encountered in the 1 m square Test Trench 2 at a depth of 47 cm. Feature 1 had two sections. The 43 cm wide sloping postmold penetrated to a depth of 84 cm. Adjoining it to the west was a shallow 45 cm long pit that sloped 3 cm toward the postmold. The latter portion

Table 2.—*Characteristics and dimensions of Area 1 features.*

No.	Unit	Type	Minimum depth	Horizontal dimensions
1	T.T.2	Postmold	47 cm	47 × 43 cm
2	A	Stone hearth	50 cm	40 × 30 cm
3	C	Circular basin (historic)	30 cm	17 × 15 cm
5	B	Hearth	47 cm	28 × 25 cm
6	E	Hearth	36 cm	45 × 26 cm
9	C	Stone hearth	70 cm	70 × 70 cm
10	J	Stone hearth	65 cm	45 × 38 cm
11	B	Stone hearth	83 cm	48 × 40 cm
12	J	Hematite cluster	117 cm	25 × 20 cm

may have resulted from soil disturbance as the post was raised to a vertical position. A cluster of six unaltered hematite concretion fragments was designated Feature 12. In possible association, and less than 20 cm to the east was a 15 by 15 cm sandstone slab.

The only other feature recorded in Area 1 was a circular basin containing a mixture of prehistoric and historic items. Encountered at a depth of 30 cm and containing one fragment of window glass, one brick fragment, one rusted nail, one rusted metal ring, and 15 fragments of slag, Feature 3 may have been the remains of a recent fence post.

ANALYSIS OF UTILIZED CHERT

Abundant chert, in pebble form, was available to prehistoric man in the Allegheny River valley. Glacial meltwaters from the retreating Wisconsin ice sheet filled the Allegheny-Ohio Valley bottoms with silt, sand, and gravel brought from the north. "In the Pittsburgh area, this layer locally reached a thickness of 80 feet." (Heyman, 1970:92). Pebbles of granite and other hard stone provided raw material for ground stone tools as did chert pebbles for chipped stone tools.

Mottled gray Onondaga chert was most plentiful and the vast majority of flaked tools found in the Allegheny valley are of this material. In Area 1 of the Blawnox site, 77% of the identifiable chert debitage from all levels was Onondaga. The second most common variety, 21%, was Delaware chert which has a pale yellow color beneath a yellow-brown pebble cortex. Delaware chert thermally alters to pink and, sometimes, pale red. The remaining 2% of pebble cherts were unidentified and include a dull gray fossiliferous chert that was more common than any of the other minor forms.

Field observations made during the excavation of the deep Middle Woodland zone encountered in Area 1 suggested a temporal change

in the utilization of exotic to local chert. It was found that exotic cherts occurred more often in the deeper and, therefore, older zones and that this observation could be tested statistically in the laboratory. Chert was identified empirically as local or exotic. Flint Ridge and Cochocton County, Ohio, were determined to be the source of 59% of exotic lithic materials and 2% was yellow eastern Pennsylvania jasper. The remaining 39% of non-local chert was of unknown derivation. To test the field observations, the data from the six Area 1 excavations units were combined because of strata homogeneity.

Within the highly disturbed 0 to 25 cm level, 100% of the debitage was of locally available pebble chert. This sample consisted of 409 flakes and pebble core fragments. From 25 to 50 cm, 98% of the 925 piece sample was local. A significant percentile change occurred however in the 50 cm and below zone. Here, only 79% of the 163 examples of debitage was of local origin.

There were 43 examples of utilized flakes recovered from the same units. They are flakes of non-uniform size and shape with one or more nibbled edges. Again, the 0 to 25 cm level contained only utilized flakes made of local chert. From 25 to 50 cm, 95% were of local material, and in the lowest zone from 50 cm and below, just 33% of utilized flakes were non-exotic. For the Blawnox site, at least, the indications are that exotic lithics were being utilized to a greater extent by the early Middle Woodland tool makers than by succeeding populations. Certain tool types, to be described in the next section, were stratigraphically variable also.

Four of the five prismatic blades, all made of exotic cherts, were recovered from 90 cm or below. One small 31 mm long example was found in the 35 to 40 cm level of Unit C. Four end and side scrapers were recovered from 87 cm or below. Only one of these is made of locally available Onondaga chert. The implications will be discussed more fully below but, it is apparent that at Blawnox there was a modification of the tool industry as well as an increase in the utilization of local lithic resources during the Middle Woodland period.

MIDDLE WOODLAND ARTIFACTS FROM AREA 1

Typology indicated that the Middle Woodland occupational zone in Area 1 was at least 1.05 m deep. Thus, was presented an opportunity to investigate Upper Ohio Valley Middle Woodland artifacts within a temporal framework. Because of a lack of investigative emphasis, little has been done in the area to expand the Middle Woodland tool inventory. The following discussion will add additional data about lithic artifacts of this era with an emphasis on flaked stone tools. The small

Table 3.—*Projectile points from Area 1 with stratigraphic provenience and size attributes in millimeters.*

Type	Depth	Length	Width	Thickness
?	100–110 cm	48	32	8
?	100–110 cm	—	—	7
Manker corner notched	60–70 cm	36	31	6
?	40–45 cm	—	17	6
Manker stemmed	35–40 cm	44	26	8
Kiski notched	30–35 cm	23	15	4
Kiski notched	25–30 cm	23	15	5
?	25–30 cm	28	16	5
Kiski notched	0–25 cm	21	12	4
?	0–25 cm	35	26	7

ceramic sample will receive attention as will the largely undiagnostic ground and pecked stone artifacts.

Projectile Points

Ten projectile points or fragments were recovered in Area 1. These will be discussed in stratigraphic sequence beginning with the deepest recovered. Table 3 lists the points, the size attribute and the depth proveniences.

100–110 cm.—Of the two specimens from this level, only one is complete. It (Fig. 5a) is a corner notched point with a ground excurvate base. In contrast to the symmetrical base with its narrow deep notches, the thick blade features one steep, much retouched edge that most likely indicates a scraping and/or cutting function. The less refined opposite edge is heavily battered. The blade has a uniform thickness of 8 mm, which is 2 mm greater than the base. The artifact is 48 mm long and 32 mm wide.

Although superficially bearing some resemblance to the St. Charles point (Bell, 1960:82–83) in basal treatment, this Blawnox specimen (and others noted by this investigator) does not possess the convex blade edges and superior workmanship of this Late Archaic and Early Woodland type. One or a few examples cannot be designated a type but it is believed that corner notched points of this configuration can be attributed to Upper Ohio Valley Middle Woodland.

A basal fragment of a corner notched point (Fig. 5b) was found at the same level. The unground base of this point is straight. The mottled light gray chert is of unknown origin.

60–70 cm.—A Manker Corner Notched point (Fig. 5c) with a rounded, unground base was found in the 60–70 cm level. It is made of mottled off-white and tan chert of non-local origin. Meticulous edge

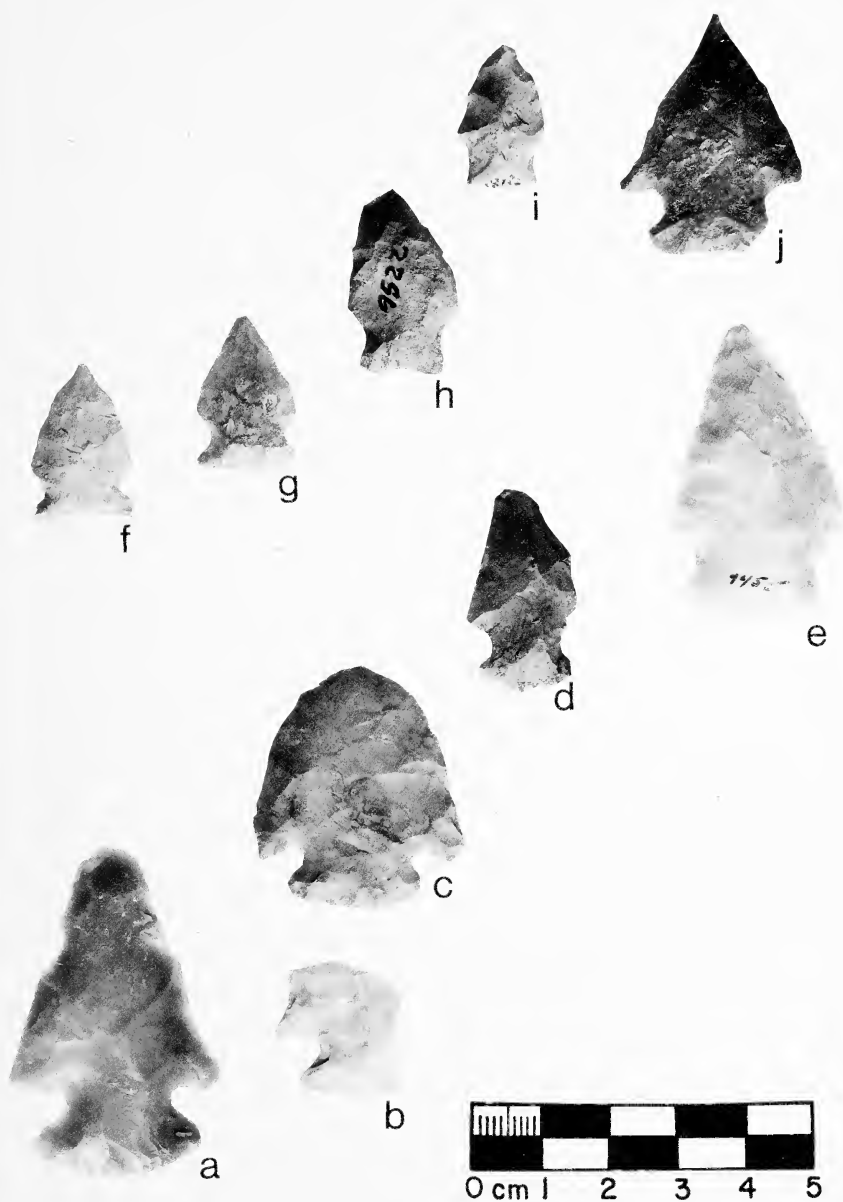


Fig. 5.—Projectile points from Area 1 illustrated by level from the bottom to the top: a-b) untyped corner notched points; c) untyped side notched point; e) Manker Stemmed Point; f-g, i) Kiski Notched Points; h) untyped expanded stemmed point; j) untyped corner notched point.

preparation and a lack of a well defined tip suggests a hafted knife function for this symmetrical tool. It is 36 mm long, 31 mm wide, and 6 mm thick in the central area of the blade. The Manker Corner Notched point has been identified on Hopewellian sites in Illinois (Montet-White, 1968:71-73). It is considered as a "smaller counterpart of the typical Snyders points" (Montet-White, 1968:71). They are believed to be more common in the Upper Ohio Valley than previously suspected.

40-45 cm.—This level contained a small rather non-descript side notched point of Delaware chert (Fig. 5d). The asymmetrical appearance may have been due to damage inflicted on the blade during use. One blade edge is completely missing and the opposite side is uneven and asymmetrical. The tip area is truncated. It is now 30 mm long, 17 mm wide, and 6 mm thick.

35-40 cm.—A point (Fig. 5e), identified as a Manker Stemmed type (Montet-White, 1968:73), featured an expanded stem and a slightly excurvate base that is not ground. The original base was probably symmetrical with rounded tangs, one of which is now missing. The blade is biconvex in profile and both edges are relatively straight. It is made of mottled gray/tan chert that may have originated in northern Ohio. It is 44 mm long, 26 mm wide, and 8 mm thick.

30-35 cm.—In the 30-35 cm level was a small, symmetrical side notched point (Fig. 5f) made of Onondaga chert. It is a Kiski Notched point, a type recently recognized by the author based on examples found at the Murphy's Old House Site, 36AR129 (George, Undated a), located on an Allegheny River floodplain in Armstrong County, Pennsylvania (see Appendix). Although there is some variance of basal treatments, all Kiski Notched points share the attribute of diminutive size. The Blawnox example here described has slightly scalloped edges and a roughly finished base. It is 23 mm long, 15 mm wide and 4 mm thick.

25-30 cm.—A point from this level bears a very close resemblance to the Kiski Notched point previously described. This specimen (Fig. 5g) is 23 mm long, 15 mm wide but a little thicker at 5 mm. The blade edges are straight and even and the base is ground. It is also made of Onondaga chert. Both of these Kiski Notched points have gradually tapering blade surfaces that would have enhanced their penetrating qualities.

Found also between 25 by 30 cm was a small expanded stemmed point (Fig. 5h) that is 28 mm long, 16 mm wide, and 5 mm thick. The last dimension was obtained near the distal end of the blade which is asymmetrical and is missing the tip. Retouch flaking had been applied to both edges with limited success possibly because of the chert's poor

quality. Of unknown origin, the grainy chert is banded light and dark gray.

0–25 cm.—A third Kiski Notched point (Fig. 5i) made of pink Delaware chert was recovered from the 0–25 cm level. It is 21 mm long, 12 mm wide, and 4 mm thick. The asymmetrical base can be considered both stemmed and notched. Removal of several relatively large flakes on the blade had caused edge damage suggesting that the specimen was an unfinished reject.

A corner notched point (Fig. 5j) from the uppermost stratum is the only example made of gray fossiliferous pebble chert. Broad notches and prominent barbs comprise the hafting portion and the symmetrical blade constricts to a sharp point. It is 35 mm long, 26 mm wide, and 7 mm thick. Although closely resembling the Garvers Ferry Corner Notched point (see Appendix), the Blawnok specimen has larger dimensions overall. Based on the carefully flaked blade/tip area, it likely functioned as a projectile point.

A comparison of the Area 1 projectile points from deeper zones with those recovered from shallower strata can be instructive. As with debitage and utilized flakes, exotic lithic material were more prominent below 50 cm which was naturally older. Here also were found types with broader spatial relationships whereas those from the upper levels had a more local flavor. It is believed that this and other Blawnok site data can provide information concerning the relationship of Upper Ohio Valley Middle Woodland populations and their influential Hopewellian neighbors to the west. These aspects will be discussed in the last section of this paper.

Prismatic Blades

Mayer-Oakes (1955:15, 66, 67, 83, 216, 217) considered the “Flint Ridge flake knife” to be a typical Middle Woodland artifact type in the Upper Ohio Valley although he made no attempt to provide attribute details. Without a regional data base, it is therefore necessary to utilize comparative data from further afield. Blades from the McGraw site, Ross County, Ohio, were thoroughly discussed by Pi-Sunyer (1965:60–81) and the Blawnok examples will herein be compared to that Hopewellian sample. Made from extremely fine grained Flint Ridge chalcedony, prismatic blades have parallel sides, a prismoidal cross-section, a medial ridge on the dorsal face (Pi-Sunyer, 1965:61) and a moderately curved longitudinal axis. On Table 4 are listed provenience and size attributes for Blawnok prismatic blade. Of the five excavated Blawnok Site prismatic blades or fragments, four conform to the Pi-Sunyer dimensional criteria. One of these is a proximal fragment (Fig. 6a) that typically exhibits the bulb of percussion on the ventral face.

Table 4.—*Provenience and size attributes of Blawnox site prismatic blades.*

Field catalog no.	Depth	Measurements (mm)		
		Length	Width	Thickness
9533	90–100 cm	—	14	3
9535	110–120 cm	—	—	2
9479	35–40 cm	31?	9	5–6
9487–9488	90–100 cm			
	100–110 cm	53?	20	4
9490	120–130 cm	65	26	5
8568	Surface	55	25	4
8568	Surface	55	19	6

The 14 mm wide fragment is made of banded honey color chalcedony possible of Flint Ridge origin. Both edges exhibit blunting through utilization.

Intensive edge wear is also present on a small distal end fragment (Fig. 6b) made of mottled beige chert. On the dorsal surface the medial ridge is bifurcated which resulted in a flattened surface.

Another distal fragment (Fig. 6c) of off-white Flint Ridge chalcedony was recovered from the 35–40 cm level. The 9 mm wide piece has a very prominent medial ridge and it is thus between 5 and 6 mm in thickness. One edge (Fig. 6c right side) exhibits use damage in the form of minute nicks while the opposite edge is flattened over two thirds of its length.

Atypical for the small sample in several respects is a 20 mm wide by 53 mm long prismatic blade with its distal end missing (Fig. 6d). It is made of unidentified pale green chert with one linear gray inclusion. The dorsal surface was multi-faceted rather than having a single medial ridge. One edge near the proximal end is retouched for a length of 12 mm (Fig. 6d left) and the rest of the edge has been nicked by use.

The only complete blade (Fig. 6e) is both wider, 26 mm, and longer, 65 mm, than those recorded from the McGraw site (Pi-Sunyer, 1965:64). It has a prominent medial ridge and is curved on its longitudinal axis. Both edges exhibit extensive wear damage over their entire lengths. The tool is made of a less than high quality off-white Flint Ridge chalcedony.

Two prismatic blades collected from the surface serve to illustrate the somewhat atypical lithics of the sample. One example (Fig. 6f) made of unidentified fine grained “butterscotch” colored material otherwise conforms to the McGraw sample. Again, both edges are nicked from use. It is 55 mm long and 25 mm wide. One other artifact (Fig. 6g) may represent utilization of locally available chert for the prismatic

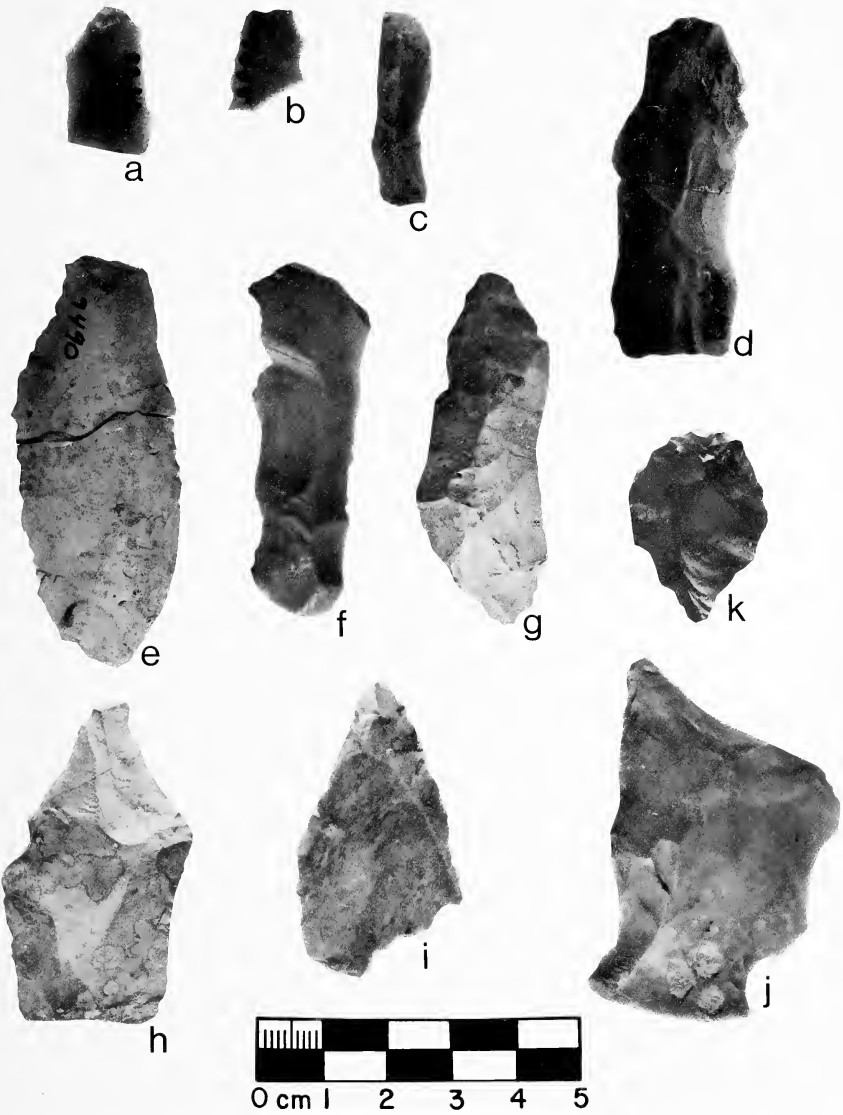


Fig. 6.—a-e) Prismatic blades from Area 1; f-g) surface collected prismatic blades; h-j) Area 1 side scrapers; k) end scraper.

Table 5.—*Depths and measurements of Blawnox site scrapers.*

Field catalog no.	Depth	Measurements (mm)		
		Length	Width	Thickness
Pointed side scraper 9534	100–110 cm	51	32	7
Pointed side scraper 9466	110–120 cm	42	26	4
Pointed side scraper 9462	80–90 cm	58	37	6
End scraper 9462	80–90 cm	30	22	6

blade stereotype. Made of Onondaga chert, the blade otherwise possesses all of the characteristic attributes. One edge, however, exhibits moderate retouch which is present only on the ventral surface. The blade is 55 mm long and 19 mm wide.

The prismatic blades from Blawnox, while generally conforming to the dimensional attributes of the McGraw site sample, are atypical of the genre. The fine grained white or pink flint, usually of Flint Ridge origin, as described by Pi-Sunyer (1965:60, 79) was used for only one of the Blawnox blades while the remainder are made of less than high quality lithic materials. It should be noted here that a majority of excavated specimens were recovered from 90 cm or below and thus the earlier strata.

Scrapers

Four scrapers were recovered in Area 1 and all were fashioned from relatively thin flakes. Three of these are morphologically similar in that all are side scrapers with one "pointed" end and multiple-edge retouch and the fourth is an end scraper. Proveniences and measurements of Blawnox site scrapers appear in Table 5.

The pointed side scraper from the 100–110 cm level is made from a spall of locally available Onondaga chert (Fig. 6h). Retouch had been applied to all edges except for the proximal end, with its bulbs of percussion, and the blunt distal end "tip." It is 51 mm long, 32 mm wide, and 7 mm thick. Evidence of retouch, in the form of fine flake removal, is exhibited on both dorsal and ventral surfaces suggesting that the tool had more than one contrived motion set. None of the other in the sample has this attribute.

From the 110–120 cm level came another flake side scraper (Fig. 6i) made of exotic mottled gray chert. Retouch had been applied to both lateral edges that converge to a point that was originally the proximal end of the flake. The longitudinal axis is curved and there is a medial ridge on the dorsal surface much like the prismatic blades. It was 42 mm long, 26 mm wide, and 4 mm at its thickest.

A similar but larger flake side scraper (Fig. 6j) with a curved longi-

Table 6.—*Depths of grit and limestone tempered pottery found in Area 1.*

Level (in cm)	Grit tempered		Limestone tempered	
	Rim	Body	Rim	Body
20-25		1	1	1
25-30	1	3		1
30-35			1	3
35-40		2		

tudinal axis and a dorsal surface medial ridge was recovered from 87 cm below the surface in Unit B. It is made of gray/tan Flint Ridge chalcedony. The left edge (Fig. 6j), from the point for a length of 42 mm, is extensively retouched creating a gradually curving surface. The shorter opposite edge is steep and only slightly retouched. The scraper is 58 mm long, 37 mm wide, and 6 mm thick.

Also from the same level and unit as the above specimen is a small end scraper (Fig. 6k) that is 30 mm long, 22 mm wide, and 6 mm thick. It is made of exotic black chert, possibly Upper Mercer. The semi-steep working edge was produced by secondary retouch flaking but heavy usage seemingly caused the edge to have become uneven or saw-toothed.

Upper Ohio Valley archaeologists have long considered the small "thumbnail" end scraper to be a diagnostic Middle Woodland artifact. Attribute analysis has not been forthcoming due to the lack of an adequate stratigraphically documented sample. The "pointed" flake side scraper herein described cannot as yet be designated an Upper Ohio Valley Middle Woodland tool type based on the limited Blawnox sample. The presence of the several specimens in the deeper, earlier zones at Blawnox should be noted.

Ceramics

Eleven body sherds and three rim sherds comprise the limited ceramic sample from Area 1. All were found in the upper levels from 20 to 40 cm below surface. Table 6 shows the depths for sherds recovered in Area 1. Although the sherd sample is small and in poor condition, a few points can be made about the pottery that was recovered from a 20 cm thick zone and ranged in size from 50 by 29 mm to 18 by 10 mm.

Limestone Tempered Ware

One of the two limestone tempered rims has an eroded exterior surface. The lip is rounded and cord impressed and the interior surface is smoothed over cordmarking. The other rim, which was 19 mm long

and 18 mm wide, has a rounded plain lip and lip paralleling cord marking. The interior surface is plain and the sherd has a thickness of 8 mm. It is classified as Watson Cord Marked, an unembellished limestone tempered ware attributed to Upper Ohio Valley Middle Woodland by Mayer-Oakes (1955:193–195). Three of the body sherds have interior-exterior cordmarking and thicknesses vary between 7 and 9 mm. The largest is only 27 by 20 mm in size. The remaining limestone tempered sherds are too fragmentary to adequately describe. Sizes vary between 18 by 8 by 8 mm to 15 by 11 by 4 mm.

Pottery featuring interior-exterior cordmarking and limestone tempering was considered by Mayer-Oakes (1955:184–190) to be a less common variety of Half-Moon Cordmarked ware with Early Woodland affinities. The Blawnox evidence plus data from the Reider site, 36WA103, indicated that interior-exterior cordmarked pottery was also a product of Upper Ohio Valley Middle Woodland potters. Feature 16 at Reider had a corrected C¹⁴ date of A.D. 420 ± 80 (Gak 5355) and contained grit tempered sherds with interior-exterior cord impressions (Stanley Lantz, personal communication). Reider was located on a Allegheny River floodplain in Warren County, Pennsylvania.

Grit Tempered Ware

Three of seven grit tempered sherds are complete enough to describe. An 8 mm thick rimsherd with a rounded, plain lip is tempered with angular fragments of sandstone. It has a plain interior surface and partially obliterated exterior cord marking that is oblique to the lip that is 15 mm long. It can best be defined as Mahoning Cord Marked. Mayer-Oakes (1955:191–192), considered the type “rather amorphous” with “a wide range of cultural and temporal differences.” A Mahoning Plain body sherd was also found. It is tempered with angular sandstone fragments and has plain interior and exterior surfaces. It is 10 mm thick and 36 by 24 mm in size.

Crushed sandstone was used for tempering in a curved, 50 by 29 mm, body sherd with exterior cord marking and interior decoration that may be fabric impressed as suggested for Middle Woodland pottery of northwestern Pennsylvania by Johnson et al. (1978:46). More of the vessel would be needed to determine the interior pattern. The body sherd, with a 12 mm thickness, is another example of Middle Woodland pottery, as described above, that resembles Half-Moon Cord Marked wares of the Upper Ohio Valley. None of the four remaining grit tempered sherds have both interior and exterior surfaces intact. Two have plain interiors and a third exhibits cordmarking. Sizes ranged from 28 by 27 by 10 mm to 18 by 16 by 6 mm.

Ground and Pecked Stone Tools

Ground stone artifacts were rare in Area 1 and all were too fragmentary to be diagnostic. A celt fragment of granite was found in the 30–35 cm level. All that remains is a portion of the bit that was 25 mm thick suggesting that it was originally a large and heavy tool. The 35–40 cm level contained a ground stone artifact fragment with a flat ventral and a rounded dorsal surface. All extant surfaces exhibit abrasion scratches. The fragment is 14 mm at its maximum thickness and would have had an estimated width of 32 mm. It was of greenstone.

Pebble hammerstones, pitted stones, numerous utilized stones of unknown function, and a few rubbed hematite concretion fragments occurred throughout the various Area 1 levels. Reddened fire spalled pebbles were common especially in the upper levels. The only “nutting stones” found during the excavation were all within the 60–75 cm level of Unit K. All have one symmetrical pit that is generally round with sloping sides and even surfaces. Two are on sandstone pebbles with maximum dimensions of 214 and 135 mm. The pits have 35 and 32 mm diameters respectively. On the latter the pit is partially obliterated by a longitudinal fracture that could indicate a heavy duty function. The third example has a single 27 mm diameter pit that indents a fire reddened sandstone slab with a length of 180 mm, a width of 118 mm and a thickness of 53 mm. Three pitted stones were also found at the same level of Unit K but there was no in situ clue to their function. Only two flint flakes were found in the same level of the unit.

AREA 2 DIAGNOSTIC ARTIFACTS

Because none of the Area 2 excavation units were dug below 50 cm, stratigraphic information is limited. Two adjoining units, F and I paralleled the river-side edge of the second terrace (Fig. 2) and here the upper zone stratigraphic composition was found to be similar to that of Area 1. In both units, the 0 to 35 cm zone contained a mix of recent and prehistoric artifacts suggesting that it was plow disturbed. No historic material was recovered below 35 cm in Unit F that was dug to 50 cm below the surface. Units G and H were not excavated below sterile zones underlying 20 and 21 cm, respectively, because of time limitations.

Six Late Woodland triangular projectile points were recovered in Area 2 and all were within the 10 to 20 cm zone of Units F and I. Depths and size attributes of these points are listed on Table 7.

The three intact triangles (Fig. 7a) exhibit little size differences with lengths between 19 and 21 mm and widths between 15 and 12 mm. A fourth specimen (Fig. 7b) is missing one tang and two others have

Table 7.—*Depth proveniences and size attributes of Area 2 triangular projectile points.*

Field catalog no.	Depth	Dimensions (mm)		
		Length	Width	Thickness
9503	15–20 cm	21	12	3
9503	15–20 cm	19	15	4
9514	10–15 cm	21	14	4
9503	15–20 cm	20	—	3
9514	10–15 cm	—	15	4
9506	10–20 cm	—	—	4

missing tips (Fig. 7c, d). One of the points is made of Delaware chert (Fig. 7d); the remainder are of Onondaga chert. All six are between 3 and 4 mm in thickness. Associated with Late Woodland Monongahela sites in southwestern Pennsylvania, these triangular points are typed as Madison points (Ritchie, 1961:33, 34, 88). Research in progress by the author would further indicate that the Blawnox specimen would be relatively late in the sequence based on their sizes.

Area 2 Middle Woodland artifacts included one pottery sherd and three projectile points. One of the latter is a small expanded stemmed point from the 10–15 cm level (Fig. 7e). Made of pink Delaware chert, the point is 24 mm long, 20 mm wide, and 5 mm thick. It possesses the characteristic flared stem, unrefined base, prominent shoulders, and relatively wide blade of the Garver's Ferry Corner Notched Point (see Appendix). The Blawnox example has damaged shoulders that are more often perpendicular to the stem on intact examples of the type.

A small relatively thick side notched point with a missing tip (Fig. 7f) was in the 25–35 cm level. It is 5 mm thick, 16 mm wide, and 16 mm long. The hafting element features symmetrical incipient notching, crudely defined tangs, and an unground incurvate base. The blade is too fragmentary to adequately describe although one edge is symmetrically bifacial. Although similar to the Kiski Notched type described above, this point is much thicker and cruder. It is made of Onondaga Chert.

Another point from the same level (Fig. 7g) is made of unidentified homogeneous gray chert. It is a symmetrical artifact with small side notches and an excurve base that is ground. Both excurve blade edges are finely serrated and the blade has a biconvex cross-section that tapers to a well defined tip. It is 46 mm long, 25 mm wide, and 8 mm thick. It is believed to be of Middle Woodland origin although the type is apparently not common in the Upper Ohio Valley.

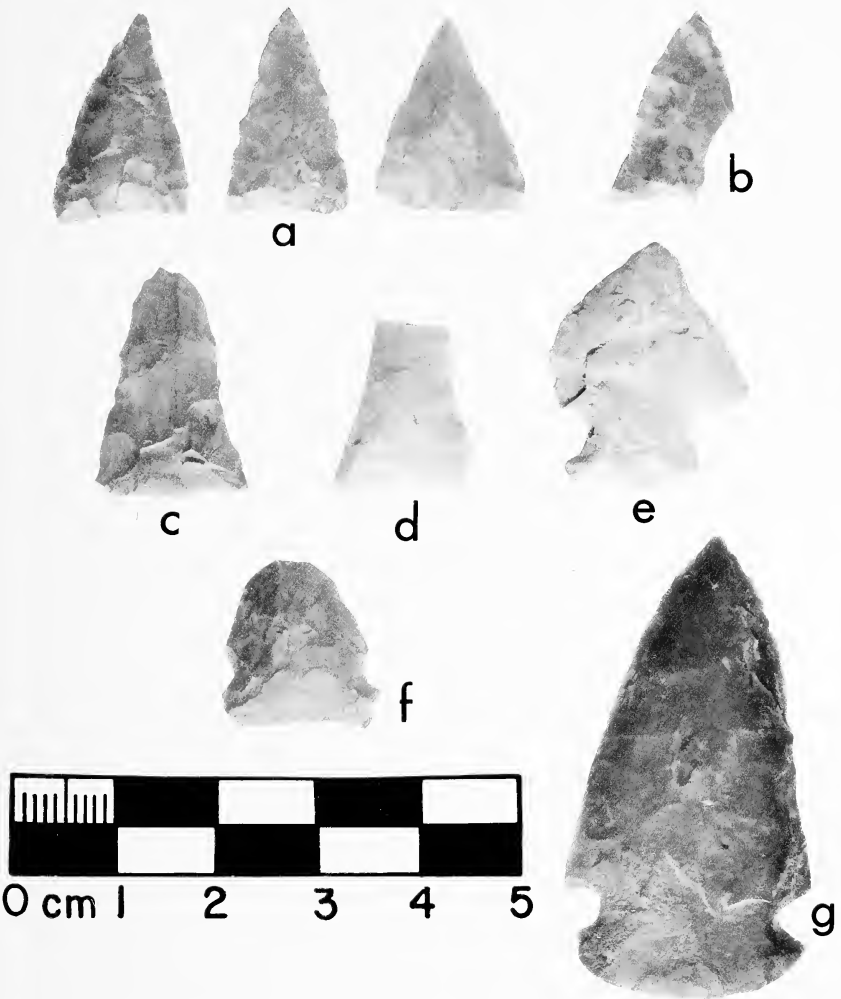


Fig. 7.—Area 2 artifacts: a-d) Late Prehistoric triangular points; e) Garvers Ferry Corner Notched Point; f) untyped side notched point; g) untyped Middle Woodland side notched point.

The above two points were found in the same 25–35 cm level of Unit 1 as a grit tempered pottery lug fragment. The exterior surface is cord-marked and it is tempered with crushed sandstone. Although it is too fragmentary to determine its true size, the diameter of the extant sur-

face is 29 mm. It is believed to be another Half-Moon ware sherd as described for Area 1 and of Middle Woodland derivation.

DISCUSSION

Mayer-Oakes (1955) and others demonstrated the existence of a recognizable Middle Woodland component in the Upper Ohio Valley that had spatial relationships to Hopewellian manifestations to the west. Little, however, has been done since to expand the understanding of these relationships. When such subjects as Middle Woodland settlement systems and environmental adaptation strategies are being pursued elsewhere in the east, Upper Ohio Valley archaeologists are still concerning themselves with typology and chronology. This is why it is believed that the meager Blawnox artifact sample, that was nonetheless stratigraphically delineated, is of significance.

Seeman (1979:406) quoting Munson noted that Havana (Illinois) Hopewell sites were often located on floodplains adjacent to the mouths of secondary streams. With its location just upstream from Squaw Run, the Blawnox site had a similar orientation. Unfortunately little else can be said about the site's settlement pattern because of the impact of recent disturbance to a floodplain greatly reduced in size by bank erosion. The quantity of surface collected Middle Woodland artifacts and the implied size of the prehistoric floodplain would suggest that Blawnox was a significant Middle Woodland settlement. Lack of data prevents defining functional settlement type as has been done by Struever (1968:307-308) for Illinois.

The existence at Blawnox of a relatively deep stratigraphic sequence attributed to Middle Woodland did, however, provide an aperture through which one could begin to delineate sequential variation. Exotic lithic materials, especially Flint Ridge chalcedony, is the most revealing evidence of Hopewell Interaction Sphere participation for a non-mortuary Upper Ohio Valley locus such as Blawnox. When the use of these and other exotic flint declined as was revealed by the Area 1 data, the implications reached beyond the site and the region. The Blawnox data thus provided more evidence to the termination of the Hopewell Interaction Sphere that Dragoo (1963:293) and others have shown to have occurred around A.D. 400-500.

The change in chert utilization corresponded with a recognizable shift in projectile point patterns that, again, had broad cultural inferences. During the paramountcy of the Interaction Sphere, distinctive point types with wide spatial distribution were a part of the Middle Woodland tool kit. Significantly, many were manufactured of exotic cherts that indicated spatial linkage. It is suggested that the upper level provenience of the Kiski Notched points in Area 1 reflected a transition that occurred in the Upper Ohio Valley and elsewhere. Prufer et al.

(1965:136) saw a "reemergence of the diverse local-regional cultural traditions, now stripped of their seemingly unifying Hopewellian overlay" in his discussion of the McGraw Site in Ohio. A similar change occurred during the Middle Woodland period in Illinois. Interestingly, Montet-White (1968:180) suggested "that this evolution reflects the adaptation of chipped-stone points to lighter and narrower shafts." She also noted that these later and smaller Middle Woodland points were made of poorer quality chert.

The distribution of Kiski Notched points beyond the middle and lower Allegheny River valley is, at present, unknown. It may be significant that a type with similar dimensional attributes, the Raccoon Notched point (Mayer-Oakes, 1955:81, 84, 91, 154, 216), does not occur at Blawnox nor other sites in the area. Perhaps this distributional pattern, supplemented with other data, might in the future be utilized to isolate distinct Upper Ohio Valley Middle Woodland cultural entities, if indeed they should continue to be given that designation.

Although the issue has been confused by terminology, many archaeologists have designated the period from approximately A.D. 300 or 400 to A.D. 1000 (Fitting, 1978:52) as the early Late Woodland period. It followed the decline of Hopewell and was characterized by an emergence (or re-emergence) of local or regional material culture expression. Some have seen it as a period of little innovation (Fitting, 1978:56) before the ascendancy of Mississippian. Perhaps it would be better to describe it as a period of decreased interaction with long distance resource centers that involved socio-economic influences that were inherent in the Hopewell Interaction Sphere. Like other local Middle Woodland populations, Upper Ohio Valley people were forced to fall back on their own resources—both physical and cultural.

In the past, there has been little evidence in the Upper Ohio Valley of a similarly conceived early Late Woodland period that was distinct from Hopewell related Middle Woodland and Late Woodland Monongahela (Fitting, 1978:55). Now it is known that Monongahela did predate A.D. 1000 based on several C^{14} dates from the Gnagey site in Somerset County (George, Undated *b*). The Blawnox data herein presented suggests that there was also, in the Upper Ohio Valley, a period that could be termed early Late Woodland. Whether or not subsequent research will precipitate the designation of this cultural manifestation as a distinct complex cannot be known at this time.

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APPENDIX

Three Upper Ohio Valley Middle Woodland Point Types

Garver's Ferry Corner Notched.—The distinguishing attributes of the Garver's Ferry Corner Notched point (Fig. 8) are as follows: a thin triangular blade with straight to slightly excurvate edges that are bifacially prepared by fine secondary flaking; prominent shoulders and symmetrical corner notches (although some bases could be considered expanded stemmed); a bifacially thinned flat base; a length of less than 30 mm. It is obvious also that the flint knappers were attempting to achieve a flat cross-section although there is some deviation from this theme.

Following are the dimensions of 11 illustrated Garver's Ferry Corner Notched points:

Example	Site	Length (mm)	Width (mm)	Thickness (mm)
a	36 Ar 129	25	25	5
b	36 Ar 129	26	23	6
c	36 Ar 129	29 (?)	22 (?)	4
d	36 Ar 129	—	20	4
e	36 Ar 19	28	21	5
f	36 Wm 30	26	21	6
g	36 Wm 30	27	21	5
h	36 Al 19	26 (?)	17	5
i	36 Al 19	25	20	5
j	36 Al 19	27	19	5
k	36 Al 19	29	21	4
	Mean	27	21	5

The type is named for the Garver's Ferry site, 36WM30, located on a Allegheny River floodplain approximately 25 km upstream from the Blawnox site. Examples f and g (Fig. 8) were collected from the site's surface while h through k are from Blawnox. The remaining examples were all collected on sites on or near the Allegheny River. Examples d and h (Fig. 8) were made of exotic cherts while the remainder were of locally available pebble cherts. The spatial distribution of the Garver's Ferry Corner Notched point beyond the middle to lower Allegheny River valley is unknown. It is quite likely that this Middle Woodland or early Late Woodland form does not occur over a wide geographic area. The occurrence of a single specimen in the 10–15 cm level of Area 2 could indicate that it is late within the sequence.

Kiski Notched Point.—Another projectile point type that has been found on some Upper Ohio Valley sites with Middle Woodland affinities is the Kiski Notched point. Its most distinguishing attribute is its diminutive size (Fig. 9). Following are the dimensions in millimeters of the illustrated Kiski Notched Points:

Example	Site	Length (mm)	Width (mm)	Thickness (mm)
a	36 Ar 129	20	14	4
b	36 Ar 129	23	18	4
c	36 Ar 129	26	15	5
d	36 Wm 140	19	14	4
e	36 Wm 140	18 (?)	16	5
f	36 Wm 140	21 (?)	16	5
g	36 Al 19	19	16	4
h	36 Al 19	20	12	4
i	36 Al 19	19	18 (?)	5
j	36 Al 19	18	16	4
k	36 Al 19	25	18	6

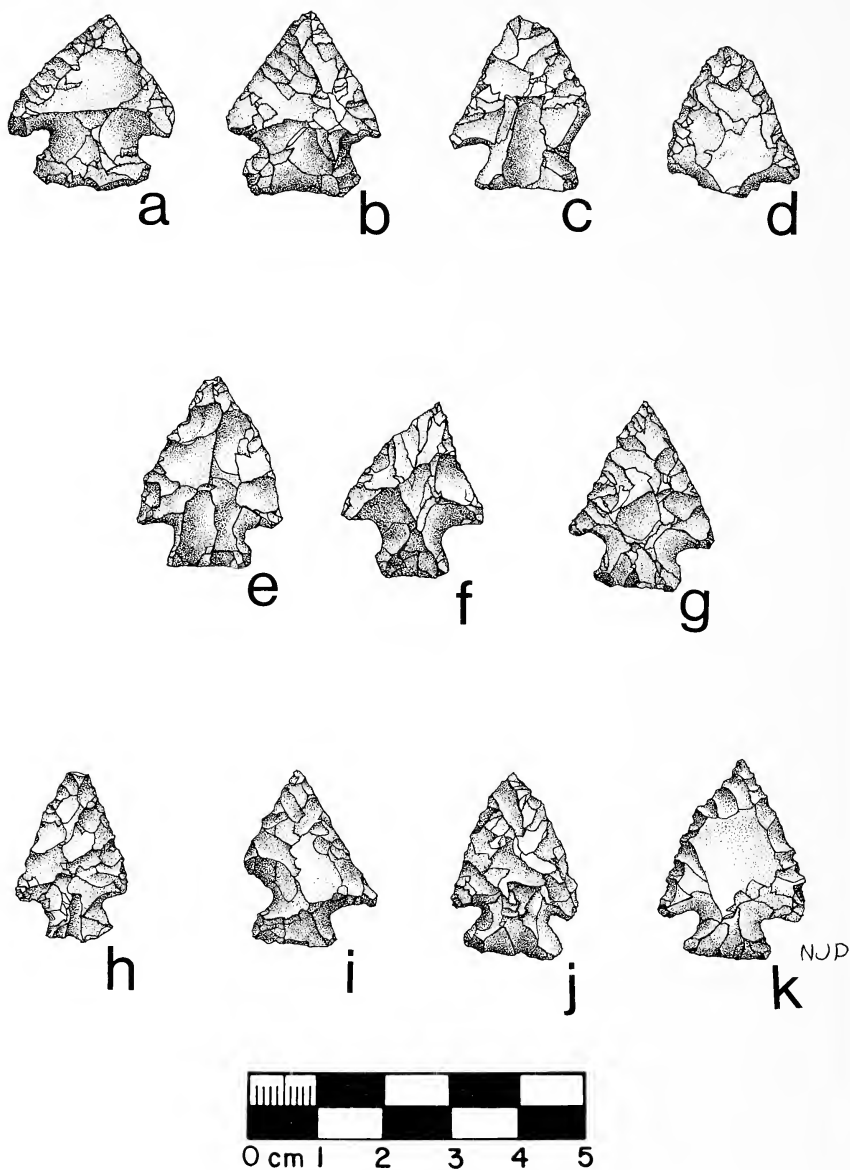


Fig. 8.—Garvers Ferry Corner Notched Points.

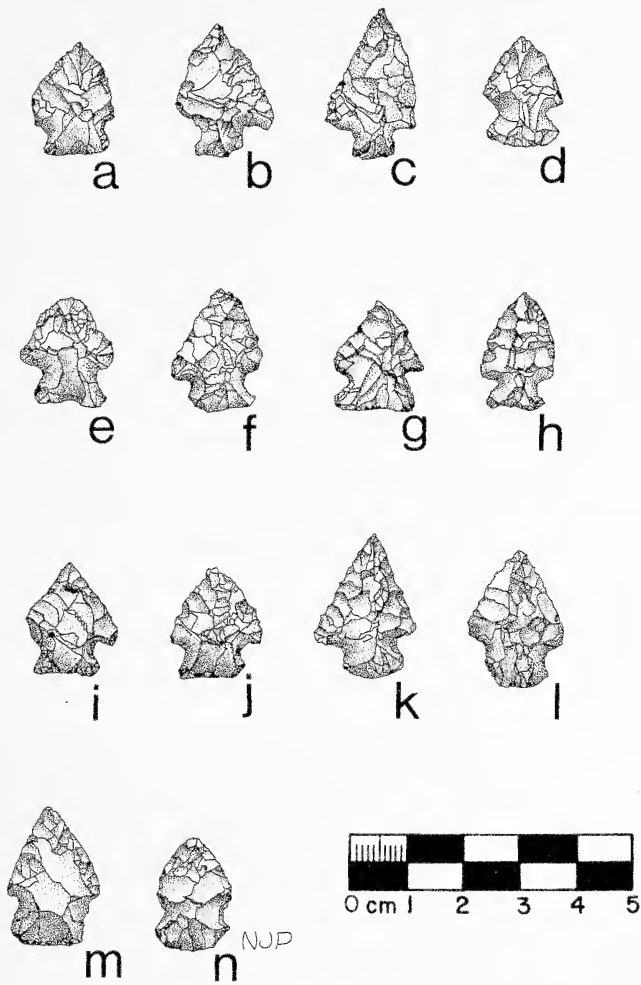


Fig. 9.—Kiski Notched Points.

Example	Site	Length (mm)	Width (mm)	Thickness (mm)
l	36 Wm 23	23	16	5
m	36 Wm 23	24	16	5
n	36 Wm 23	19	13	5
	Mean	21	16	5

Although Kiski Notched points seem not to fit a tight typological template, especially in basal treatment, there are other distinguishing attributes. All are apparently made from a prepared biconvex preform rather than a flake. Blade edges are straight to slightly convex and they do not exhibit flattening or use scarring as one might expect if the tools

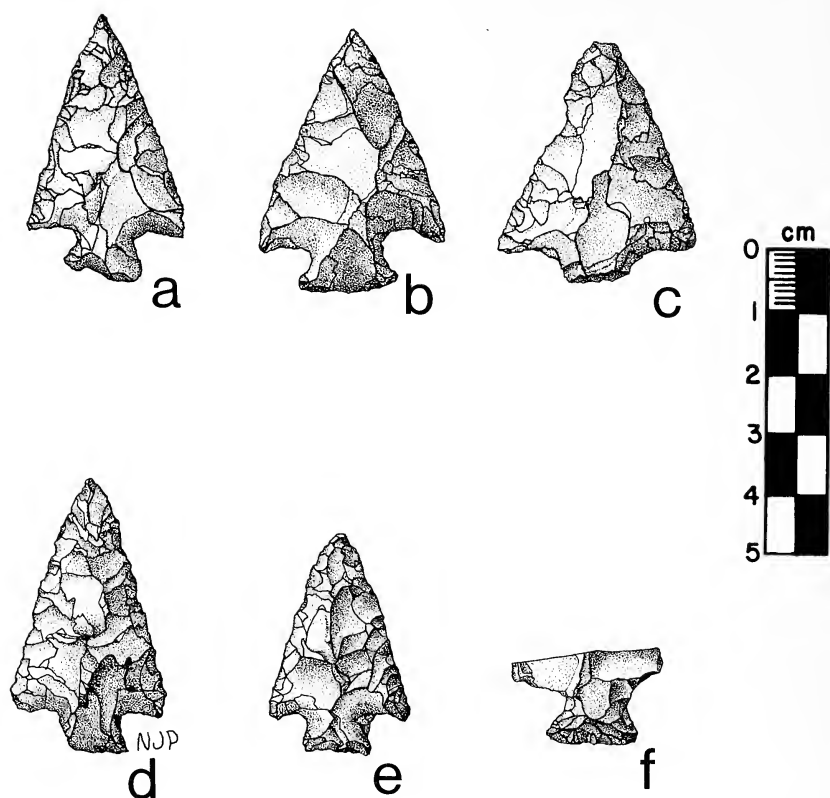


Fig. 10.—Murphys Stemmed Points.

were used as hafted knives. Most examples are only a few millimeters longer than they are wide and the overall impression is one of stubbiness. Most of the bifacially thinned bases are straight to slightly concave although there are some that exhibit indented bases (Fig. 9e). Most of the examples are corner notched although side notching (Fig. 9n) and incipient stemming (Fig. 9l) can be noted for some specimens.

Both exotic and local lithic materials are used in the manufacture of the illustrated points. Examples a, e, and j are of various shades of Flint Ridge chalcedony and examples e and f (Fig. 9) are also of exotic chert of unknown origin. Pebble derived Onondaga, Delaware, and fossiliferous chert were used for the remaining examples.

The Kiski Notched point is considered to be of late Middle Woodland affiliation based on the Area 1 Blawnox evidence. The distribution of the type apparently extends beyond the middle and lower Allegheny valley. Six of the illustrated points were from two upland sites in Westmoreland County, the Ryan site, 36WM30, and the Thomas Orr site, 36WM140. Thus, their distribution extends southeast of the Allegheny River for at least 34 km, the measured map distance to Thomas Orr.

Murphys Stemmed Point.—Seemingly less common than the two previously described types, the Murphys Stemmed point type has not been recorded for Blawnox. The type

(Fig. 10) has the following attributes: a broad triangular blade with straight edges except near the tip when they become slightly convex; a flat biconvex cross-section; prominent generally "pointed" shoulders; and a symmetrical expanded stem with a flat base. Following are the mm dimensions in millimeters of the illustrated examples:

Example	Site	Length (mm)	Width (mm)	Thickness (mm)
a	36 Ar 129	42	25	6
b	36 Ar 129	41	30	7
c	36 Wm 23	?	32	7
d	36 Wm 140	42	25	6
e	36 Wm 140	35	23	6
f	36 Ar 20	?	24	?
	Mean	40	27	6

The makers of Murphys Stemmed points apparently preferred high quality lithic materials such as Flint Ridge chalcedony. Examples a, c, and f (Fig. 10) are made of this material while b and d are of unidentified exotic chert. Only e (Fig. 10) was made of locally available tan Delaware chert. Like the Kiski Notched points previously described, the Murphys Notched point occurs both in the middle Allegheny valley and on upland sites to the southeast in Westmoreland County. The full extent of its distribution is, at present, unknown as is its temporal placement in Upper Ohio Valley Middle Woodland, although the occurrence of the type on sites that also contain Kiski Notched points may be significant.

Discussion.—The Blawnox excavation provided the first stratigraphic evidence that the Garvers Ferry Corner Notched and Kiski Notched points were of late Middle Woodland origin. The occurrence of these and Murphy's Stemmed points on sites with Middle Woodland affinities was, however, recognized earlier. The association of small, thin projectile points with late Middle Woodland components is suggestive of a change in weapon technology, that is similar to that proposed by Montet-White (1968:180) for Illinois as "the adaption of chipped stone points to lighter and narrower shafts." A more concrete hypothesis may relate this happening to the introduction of the bow and arrow.

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ARTICLE 11

DENTAL VARIATION IN *MICROTUS XANTHOGNATHUS*, *M. CHROTORRHINUS*, AND *M. PENNSYLVANICUS* (RODENTIA: MAMMALIA)

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ABSTRACT

Variations of the occlusal pattern in M^3 s of *Microtus xanthognathus* (Leach), *M. chrotorrhinus* (Miller), and *M. pennsylvanicus* (Ord) were studied and compared to test their taxonomic value. Comparative data are presented in tabular form. There is a negative correlation between increasing complexity of M^3 and intrinsic variation that operates independently of species. It is suggested that this indicates a reduction in phenotypic variation as the M^3 approaches its functional limit of complexity and the pattern becomes genetically "fixed." *M. xanthognathus* has the simplest occlusal pattern of M^3 , *M. chrotorrhinus* the most complicated, whereas *M. pennsylvanicus* has the broadest range of variation. The occlusal pattern of M^3 may show such variation that individuals of any of the three species may occasionally have identical occlusal patterns. Recourse to statistical probabilities in large samples of isolated M^3 s in paleontological sites facilitates referral to species.

INTRODUCTION

Three species of the subgenus *Microtus* (defined here as possessing first lower molars with typically five closed alternating triangles and essentially symmetrical trefoils) have been identified from paleontological deposits of Wisconsinan age in the Appalachian highlands of eastern North America—the meadow vole *Microtus pennsylvanicus* (Ord), the rock vole *M. chrotorrhinus* (Miller), and the yellow-cheeked vole *M. xanthognathus* (Leach). The first two still occur there. *M. pennsylvanicus* is a common moist-grassland species. *Microtus chrotorrhinus* is rare and local in cool, usually rocky, mountain woodlands, but *M. xanthognathus* occurs today only in the western North Amer-

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ican subarctic taiga (Hall and Kelson, 1959). These three species were common associates in late Pleistocene sinkhole/cave/raptor-roost bone deposits in the area up to ca. 11,300 yrs. BP (Guilday et al., 1964).

The present study stemmed from an attempt to identify isolated upper third molars from an early Wisconsinan fissure-fill, the Strait Canyon local fauna, Highland County, Virginia. It should be stressed that remarks throughout this paper, unless otherwise qualified, refer only to the three species discussed above and do not necessarily refer to any other species of *Microtus*.

Observations and measurements were taken on 1799 M³s—1235 from four Recent collections of *M. pennsylvanicus*, and 153 *M. cf. pennsylvanicus* from the Pleistocene of Virginia; 155 Recent and 49 late Pleistocene M³s of *M. chrotorrhinus* from Quebec and Pennsylvania, respectively; and 207 M³s of *M. xanthognathus* from the late Wisconsinan of Pennsylvania and Virginia. Observations of additional specimens were taken from the literature. Throughout this study left and right M³s were lumped for the purpose of compiling percentages. While it is possible to make paired observations in Recent skulls, it is rarely possible when dealing with collections of isolated fossil teeth. Treating all teeth, left or right as units in both fossil and Recent collections makes it possible to utilize a larger fossil sample and makes both collections more comparable. In the list of specimens examined, the number of crania examined in each sample (if known) is given, followed by a hyphen and the number of M³s examined.

Complete tooththrows present a suite of characters that make identification to species relatively easy, but isolated molars, such as are usually found in most fossil deposits, present problems. Lower dentitions of these three species are very similar (but adult *M. xanthognathus* molars are identifiable on sheer size alone) and have little practical value in taxonomic identification within the subgenus when dealing with individual teeth. The most diagnostic teeth are the upper second and third molars.

ABBREVIATIONS

The following abbreviations are used: AL = length of anterior portion of M³; PL = length of posterior portion of M³ (see text for definitions); CV = coefficient of variation; SD = standard deviation; OR = observed range; CM = Carnegie Museum of Natural History; G = author's field catalogue number; M¹–M³ = upper molars; UCM = University of Connecticut mammal collection; BU = Boston University mammal collection; BP = before present.

UPPER SECOND MOLAR

The presence or absence of the small posterior fourth triangle (posterior lingual or "*pennsylvanicus*" loop) in the upper second molar of *Microtus* is a significant and constant character. It is present in *M.*

Table 1.—*Presence or absence of posterior lingual loop of M², three species of Microtus.*

Locality	Present	Absent	Reference
<i>Microtus pennsylvanicus</i> (Ord)			
Pennsylvania	50	0	Guthrie, 1965
Ohio	82	0	Guthrie, 1965
Connecticut	53	1	Oppenheimer, 1965
		(see text)	
Virginia	523	0	Parramore Island, Merritt collection
Virginia	132	0	Comers Cave, Hamilton collection
Quebec	93	0	St. Elzear collection, CM
Summary	933	1	
<i>Microtus chrotorrhinus</i> (Miller)			
Quebec	0	155	St. Elzear collection, CM
Eastern North America	0	464	Martin, 1973
Summary	0	619	
<i>Microtus xanthognathus</i> (Leach)			
Alaska/Canada	0	28	Guilday and Bender, 1960
Pennsylvania/Virginia (late Pleistocene)	0	28	CM collections
Summary	0	56	

pennsylvanicus but not in *M. chrotorrhinus* or *M. xanthognathus* (Table 1). Its degree of development is variable but it is present in virtually all *M. pennsylvanicus* and appears to be a constant characteristic of the species (Miller, 1896). The one reported case of the absence of the lingual loop, a Connecticut specimen (Oppenheimer, 1965: Fig. 4B) was teratological. Its presence in the related Palaearctic species *M. agrestis* (Klimkiewicz, 1970) is apparently not as constant. Island populations off Denmark, in the Baltic, have been reported where the "agrestis-loop" of M² is weak or nonexistent (Ursin, 1949). The large island sample of *M. pennsylvanicus* reported on here (Parramore Island, Virginia, a small Atlantic barrier beach island—Merritt collection) had the M² "pennsylvanicus-loop" well developed, and it is also well developed in *M. breweri* (Baird), an *M. pennsylvanicus* derivative isolated on Muskeget Island, Massachusetts, by Holocene sea level changes (Tamarin and Kunz, 1974). The posterior lingual loop of M² of *M. pennsylvanicus* was presumably present in the parental Palaearctic stock from which the species evolved and has been a characteristic feature, differentiating *M. pennsylvanicus* from other North American *Microtus* since Illinoian times (Kurtén and Anderson, 1980). It is sometimes developed in *M. californicus*, however.

M. pennsylvanicus dentitions with M² present can therefore readily be identified with or without the presence of M³. Isolated M²s without

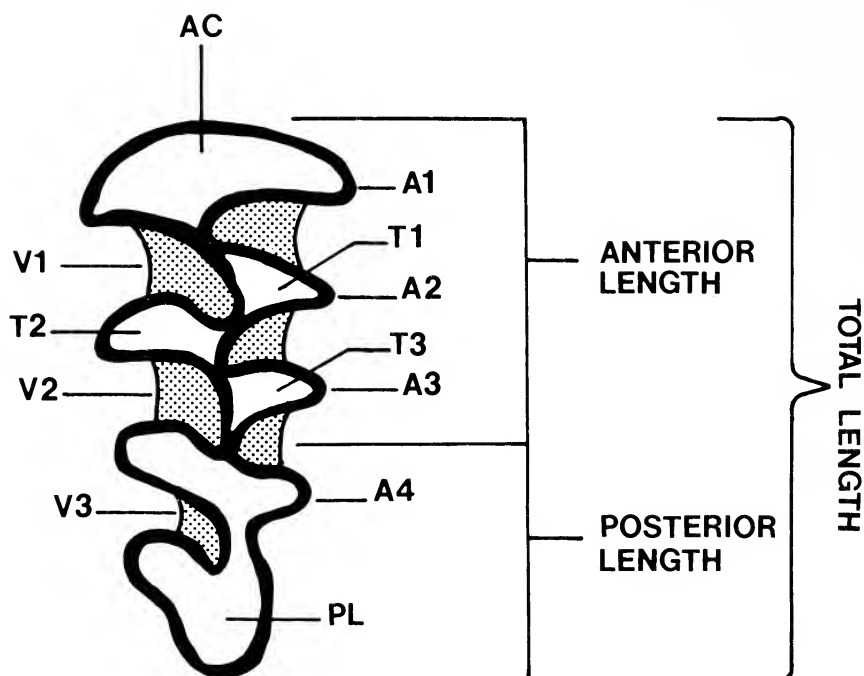


Fig. 1.—Left M^3 , *Microtus*: AC = anterior crescent, A 1–4 = labial salient angles; T 1–3 = alternating triangles; V 1–3 = lingual reentrant valleys; PL = posterior lobe. Stipple = cementum.

the small “*pennsylvanicus-loop*,” however, may be either *M. chrotorrhinus* or immature *M. xanthognathus* (or *Pitymys* or *Pedomys*) and recourse must then be made to the occlusal pattern of M^3 .

UPPER THIRD MOLAR

Basic occlusal pattern in the subgenus *Microtus* consists of an anterior crescent followed by three alternating triangles forming the morphologically conservative anterior portion of the tooth, and a highly variable posterior portion in which additional triangles and lingual reentrant valleys may be formed (Fig. 1). Six characters of M^3 were chosen for study. 1) Degree of fusion or isolation of 1st and 2nd triangles. 2) Number and degree of development of lingual reentrant valleys. 3) Number of labial salient angles. (By convention triangles, salient angles, and reentrant valleys are counted from front to back in upper molars and from back to front in lower molars.) 4) Total length of occlusal surface. 5) The relationship between the length of the an-

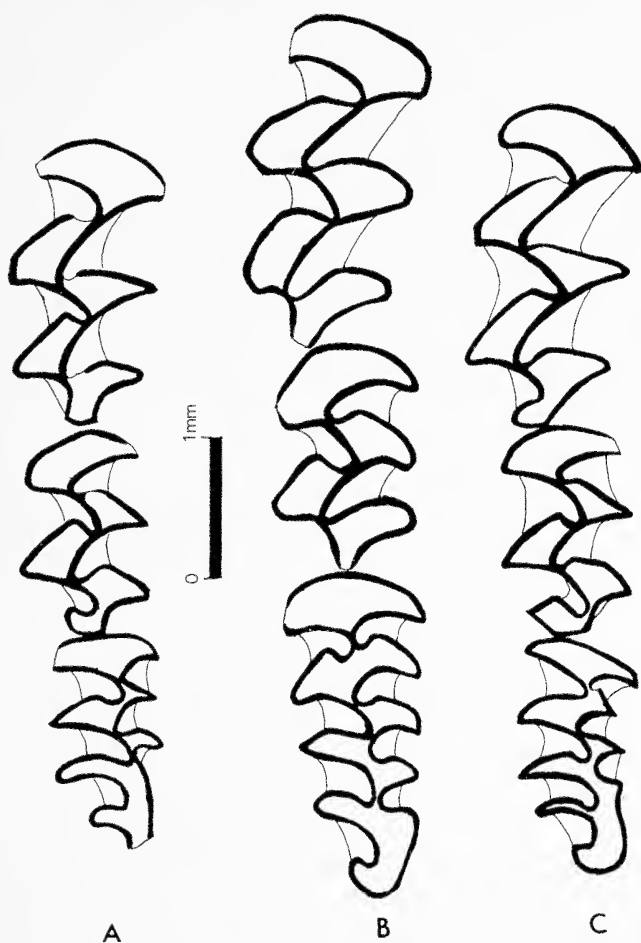


Fig. 2.—A) *Microtus pennsylvanicus* (Ord) CM 30428a, Left M^1 – M^3 . B) *Microtus chrotorrhinus* (Miller) CM 30404, Left M^1 – M^3 . C) *Microtus pennsylvanicus* (Ord) CM 30427a, Left M^1 – M^3 . (Note *chrotorrhinus*-like M^3 .) All from Caverne de St. Elzéar de Bonaventure, Gaspé, Québec, Canada, Recent.

terior conservative portion and the length of the variable posterior portion of M^3 . 6) Varying ratios of variability of anterior and posterior portions of M^3 , expressed as CV of PL/CV of AL.

Microtus upper third molars (of at least the three species under discussion) fall into two major categories—1) *M. pennsylvanicus*/*M. xanthognathus* pattern typically consisting of an anterior crescent,

Table 2.—Fusion of first and second alternating triangles (percentiles), M^3 , three species of *Microtus*.

Locality	Full or partial fusion	No fusion	N
<i>Microtus pennsylvanicus</i> (Ord)			
St. Elzéar, Québec	9.80	90.20	93
Comers Cave, Virginia	43.00	57.00	132
Parramore Island, Virginia	13.30	86.70	1000
Lumped	16.20	83.75	1225
<i>Microtus cf. pennsylvanicus</i> (Ord)			
Strait Canyon Fissure, Virginia (late Pleistocene)	46.35	53.64	151
<i>Microtus chrotorrhinus</i> (Miller)			
Eastern North America, 53 localities*	95.00	5.00	464
New Paris No. 4, Pennsylvania (late Pleistocene)	93.90	6.10	49
St. Elzéar, Québec	91.50	8.50	153
Lumped	94.14	5.86	666
<i>Microtus xanthognathus</i> (Leach)			
Alaska/Canada**	0.00	100.00	3
New Paris No. 4, Pennsylvania (late Pleistocene)**	0.00	100.00	9
Clark's Cave, Virginia (late Pleistocene)	0.00	100.00	73
Lumped	0.00	100.00	85

* Martin, 1973.

** Guilday and Bender, 1960:320, Fig. 3.

three alternating triangles which may or may not be fused, three labial angles, and three cement-filled lingual valleys (Fig. 2); 2) an *M. chrotorrhinus* pattern consisting typically of more than three alternating triangles, which may or may not be fused, from four to rarely five labial angles, and four cement-filled lingual valleys (Fig. 2). Great variation is seen in both types, however. The variation in the occlusal pattern of M^3 of *M. pennsylvanicus*, especially, is so great that it may occasionally resemble that of the M^3 of *M. chrotorrhinus* (Fig. 2). Detailed variation in the M^3 s of *M. pennsylvanicus*, *M. xanthognathus*, and *M. chrotorrhinus* is presented below.

Fusion of First and Second Triangles (Table 2)

The degree of fusion between alternating triangles 1 and 2 is unstable within the subgenus *Microtus* and varies from completely fused (Fig. 3N, O) to partially fused (Fig. 3L, M) to isolated (Fig. 3, K). This is

governed by the depth and path of the first lingual reentrant valley. In those specimens showing complete fusion, this reentrant is broadly V or U shaped, its axis at right angles to the anteroposterior axis of the tooth. But in examples with only partial or no fusion, the valley is crescent-shaped, its axis turning rearward and depressing the leading edge of the "fused-triangles" until it abuts against the posterior enamel wall of the first alternating triangle, thereby isolating the first and second triangles from each other. Occasionally, other triangles may show varying degrees of fusion. Martin (1973) has quantified them in 464 specimens of *M. chrotorrhinus* and noted the possible occurrence of fusion versus isolation at eight different loci on M^3 resulting in 21 different occlusal patterns resulting from the presence or absence of fusion alone (Martin, 1973:192, Table 1.). The most important locus, from the standpoint of interspecific variability, is the triangle 1-2 fusion (Martin's locus 9). Fusion varied from 0% in *M. xanthognathus*, to over 90% in *M. chrotorrhinus* with little intraspecific variation. Whether this character, or others discussed here, varies geographically or temporally remains to be demonstrated. That it does vary, at least randomly, can be seen by comparing the percentages of first-second triangle fusion in three large samples of *M. pennsylvanicus* (St. Elzear, Comers Cave, and Parramore Island, Table 2).

Lingual Reentrant Valleys (Table 3)

There is variation, both intra- and interspecific, in the number and degree of development of cement-containing, lingual valleys of M^3 . The simplest pattern is that of *M. xanthognathus*, the most complex is that of *M. chrotorrhinus*, whereas the most variable pattern is seen in *M. pennsylvanicus*.

The presence of only three lingual valleys is usual for *M. xanthognathus*. Only a single instance of a cement-filled fourth lingual valley was noted in 111 modern and late Pleistocene examples (also see Martin, 1973:194, Plate 5 E). Four additional specimens (3.6%) had shallow, poorly-developed fourth lingual valleys without cement, and the lingual aspect of the posterior lobe of M^3 varies from usually convex, with no trace of valley formation, to strongly concave, with incipient fourth reentrant valleys.

In sharp contrast, the fourth lingual valley in *M. chrotorrhinus* was present and fully developed in 77.8% of the 203 Recent and late Pleistocene specimens examined. As many as 94.8% of the specimens from St. Elzear, Quebec, had deep well-developed fourth lingual valleys. Martin (1973) describes this as the usual pattern in the 464 specimens he examined from throughout the animals modern range. The presence of only three lingual valleys, plus an incipient fourth, may reach high

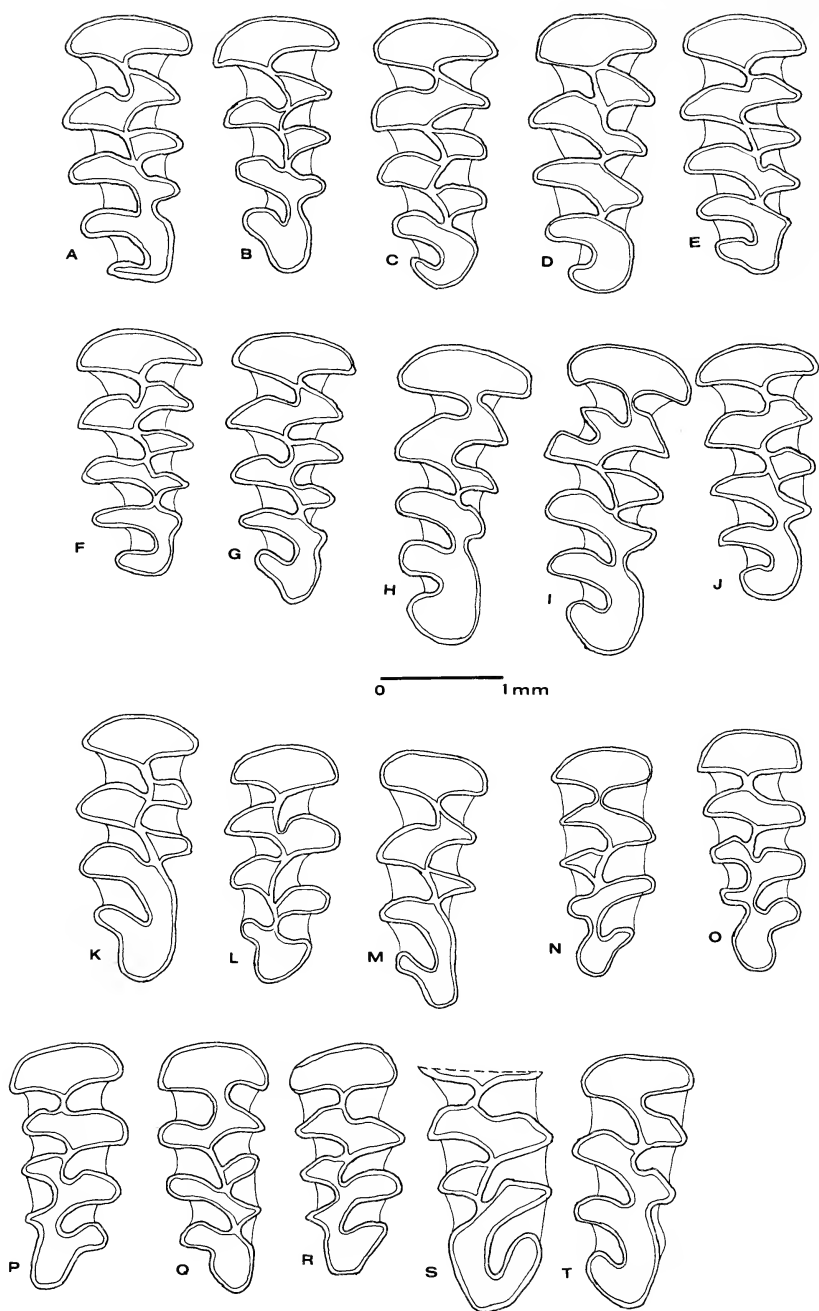


Table 3.—Percentage of occurrence of cementum-filled fourth lingual valley of *M*³, various *Microtus*.

Locality and age	Three valleys only	Fourth valley present	N
<i>Microtus pennsylvanicus</i> (Ord)			
St. Elzéar de Bonaventure, Québec, Recent	80.0	20.0	85
New Paris No. 3, Pennsylvania, Recent	77.0	23.0	13
Comers Cave, Virginia, Recent	98.0	2.0	132
Parramore Island, Virginia, Recent	96.5	3.5	1001
Combined	95.0	5.0	1231
<i>Microtus cf. pennsylvanicus</i> (Ord)			
Strait Canyon Fissure, Virginia, late Pleistocene	96.1	3.9	153
<i>Microtus chrotorrhinus</i> (Miller)			
St. Elzéar de Bonaventure, Québec, Recent	5.2	94.8	155
New Paris No. 4, Pennsylvania, late Pleistocene	35.3	64.7	49
Combined	12.3	87.7	204
<i>Microtus xanthognathus</i> (Leach)			
Alaska/Canada, Recent*	100.0	0.0	28
New Paris No. 4, Pennsylvania, late Pleistocene*	100.0	0.0	10
Clark's Cave, Virginia, late Pleistocene	98.7	1.3	73
Combined	99.1	0.9	111

* Guilday and Bender, 1960.

proportions in some populations (35% at New Paris No. 4, Pennsylvania, N = 49). Martin (1973:Plate 2, series 5, a, b, c) illustrates three such cases from the late Pleistocene New Paris No. 4, Pennsylvania, local fauna. Such high percentages may not be significant because of the small sample size, but suggest that the degree of development of the fourth lingual valley in *Microtus chrotorrhinus* may change both geographically and temporally. In most instances examined, *M. chrotorrhinus* M³s exhibit a more complicated occlusal pattern than in either *M. xanthognathus* or *M. pennsylvanicus*.

In contrast to the low incidence of the fourth lingual valley in *M.*

←

Fig. 3.—*Microtus chrotorrhinus* (Miller) Recent: Caverne de St. Elzéar de Bonaventure, Québec, Canada. A) CM 38514, left M³. B) CM 38515, left M³. C) CM 38516, left M³. D) CM 38517, left M³. E) CM 38518, left M³. F) CM 38519, left M³. G) CM 38520, left M³. H) CM 38521, left M³. I) CM 38522, left M³. J) CM 38523, left M³.

Microtus cf. pennsylvanicus (Ord) late Pleistocene: Strait Canyon Fissure, Virginia. K) CM 38505, left M³. L) specimen lost, no number, right M³. M) CM 38506, left M³. N) CM 38507, right M³. O) CM 38508, right M³. P) CM 38509, right M³. Q) CM 38510, left M³. R) CM 38511, right M³. S) CM 38512, partial right M³. T) CM 38513, left M³.

xanthognathus, and its high incidence in *M. chrotorrhinus*, its occurrence in *M. pennsylvanicus*, while low, is intermediate between the two species and highly variable as suggested by the high coefficient of variation of the posterior portion of M^3 (Table 7) of *M. pennsylvanicus* compared with the other two species. In addition, the tendency toward the incipient development of the fourth lingual valley, expressed as varying degrees of concavity of the posterior lingual wall of the tooth, is so strong in *M. pennsylvanicus* that it may be described as the usual condition; it is present in 74.2% of the Comers Cave, Virginia, sample. In this sample, 63.6% showed a slight concavity, 10.6% had the cavity deepened to the point where it could be described as a shallow valley, while an additional 2.27% had a fully developed cement-filled fourth lingual valley (Table 3); only 23.5% showed no trace of fourth lingual valley formation.

In summary, a cement-filled fourth lingual valley was present in less than 1% of the *M. xanthognathus* examined, about 4–5% of *M. pennsylvanicus*, and over 77% of *M. chrotorrhinus*. The pattern appears most stable in both *M. chrotorrhinus* and *M. xanthognathus* despite their extreme disparity, and most subject to variation in *M. pennsylvanicus*.

Labial Salient Angles (Table 4)

The number of labial salient angles varies from three to five and is correlated with tooth pattern complexity. All three species have at least three well-developed labial angles. Most *M. xanthognathus* and *M. pennsylvanicus* have three labial angles, most *M. chrotorrhinus* have four.

The simplest condition, again, is that of *M. xanthognathus*—three labial angles are the normal complement (87.7%) with a small number of specimens (12.3%) having a variable, but always rudimentary, fourth labial salient angle.

The most complex pattern is seen in *M. chrotorrhinus*, where 81.4% had four well-developed angles and an additional 17.1% had a small, poorly defined fifth labial salient angle.

Although the majority of *M. pennsylvanicus* M^3 s had three labial salient angles, 18% had an additional fourth labial angle, a percentage somewhat higher than in *M. xanthognathus*, but much less than in *M. chrotorrhinus*. A small fifth labial salient angle, such as often observed in *M. chrotorrhinus*, was not seen in either 1235 M^3 s of Recent *M. pennsylvanicus* or 113 M^3 s of *M. xanthognathus*. Variation in numbers of specimens with fourth labial salient angles was very high in *M. pennsylvanicus*, ranging from 3% (Comers Cave) to 30.7% (New Paris No. 3). The Strait Canyon sample of 152 M^3 s, referred to *M. cf. Penn-*

Table 4.—Percentage of number of labial salient angles of M^3 , various *Microtus*.

Locality and age	Three angles	Four angles	Five angles	N
<i>Microtus pennsylvanicus</i> (Ord)				
St. Elzéar de Bonaventure, Québec, Recent	83.0	17.0	0.0	89
New Paris No. 3, Pennsylvania, Recent	69.3	30.7	0.0	13
Comers Cave, Virginia, Recent	97.0	3.0	0.0	132
Parramore Island, Virginia, Recent	80.0	20.0	0.0	1001
Combined	82.0	18.0	0.0	1235
<i>Microtus cf. pennsylvanicus</i> (Ord)				
Strait Canyon Fissure, Virginia, late Pleistocene	58.5	40.2	1.3 (rudimentary)	152
<i>Microtus chrotorrhinus</i> (Miller)				
St. Elzéar de Bonaventure, Québec, Recent	0.0	79.0	21.0	155
New Paris No. 4, Pennsylvania, late Pleistocene	6.1	89.8	4.1	49
Combined	1.5	81.4	17.1	204
<i>Microtus xanthognathus</i> (Leach)				
Alaska/Canada, Recent*	85.7	14.3	0.0	28
New Paris No. 4, Pennsylvania, late Pleistocene*	91.7	8.3	0.0	12
Clark's Cave, Virginia, late Pleistocene	87.7	12.3	0.0	73
Combined	87.7	12.3	0.0	113

* Guilday and Bender, 1960.

sylvanicus, had 40.2% showing fourth labial salient angles, a percentage about twice that of modern *M. pennsylvanicus* but at the same time only 50% that of *M. chrotorrhinus*. The high percentage of fourth labial salient angles in the Strait Canyon sample may be a random mathematical artifact, or may be due to the presence of some undetected specimens of *M. chrotorrhinus* in this collection of isolated late Pleistocene M^3 s.

A corollary to variation in the number of labial salient angles is the number of cementum tracts laid down in the labial reentrants. These vary both infra- and interspecifically (Table 5). Hallberg et al. (1974) considered the high incidence of the third labial cementum tract in the M^3 of *M. pennsylvanicus* (95.4%, $N = 328$) and its apparent absence in *M. xanthognathus* ($N = 12$) to be a useful taxonomic character in distinguishing between the two species. This is corroborated in this study, but with reservations. As many as 5.2% of the M^3 s of *M. pennsylvanicus* may lack the third labial cementum tract, and as many as 10.3% of *M. xanthognathus* may have it, so that the evaluation of this character is best handled statistically and not on an individual basis. In keeping with its complicated morphology, 69.1% ($N = 55$) of *M. chrotorrhinus* M^3 s had an additional fourth labial cementum tract not

Table 5.—Percentage of number of labial cementum tracts, various *Microtus*.

Locality and age	Two tracts only	Three tracts only	Four tracts only	N
<i>Microtus pennsylvanicus</i> (Ord)				
St. Elzéar de Bonaventure, Québec, Recent	1.3	98.7	0.0	77
U.S.A., various localities *, Recent	4.6	95.4	0.0	328
Comers Cave, Virginia, Recent	5.2	94.8	0.0	97
<i>Microtus cf. pennsylvanicus</i> (Ord)				
Strait Canyon Fissure, Virginia, Pleistocene	5.6	94.4	0.0	72
<i>Microtus chrotorrhinus</i> (Miller)				
St. Elzéar de Bonaventure, Québec, Recent	0.0	30.9	69.1	55
<i>Microtus xanthognathus</i> (Leach)				
New Paris No. 4, Pennsylvania, Pleistocene	96.6	3.4	0.0	119
Clark's Cave, Virginia, Pleistocene	89.8	10.2	0.0	88

* Hallberg et al., 1974.

observed in either of the other two species; none had only two labial cementum tracts (the norm in *M. xanthognathus*).

Size (Table 6)

The total length of the M^3 in *M. pennsylvanicus* and *M. chrotorrhinus* is, for all practical purposes, identical. The M^3 of *M. xanthognathus* averages about 27% larger with a smaller coefficient of variation (taking into consideration adults only), suggesting less infraspecific variation in *M. xanthognathus* and strengthening the impression of morphological conservatism suggested by the simpler dental pattern.

Variability of Posterior Portion of M^3 Compared to Anterior Portion (Table 7)

If the M^3 is divided into two portions, an anterior portion consisting of the anterior crescent plus the first three alternating triangles (AL) and a posterior portion which includes all of the remaining area of occlusal surface (PL), it becomes apparent that most of the variation, both in form and in relative length, takes place in the posterior portion of the tooth. This was first pointed out for *M. pennsylvanicus* by Guthrie (1965). It is also true of the other two species, and may reflect the fact that the M^3 , unimpeded by additional molars, has more freedom to develop and expand caudally (Hinton, 1926). This variation, clustering around specific norms, is what is responsible for the heightened taxonomic value of M^3 in some, but not all, *Microtus*.

Table 6.—Total length (in mm) of M^3 , three species of *Microtus*.

Locality	Mean	OR	SD	CV	N
<i>Microtus pennsylvanicus</i> (Ord)					
St. Elzéar, Québec	1.90	1.59–2.35	.15	8.27	55
New Paris No. 3, Pennsylvania	1.94	1.75–2.14	.11	5.73	13
Parramore Island, Virginia	2.19	1.76–2.46	.15	6.84	50
<i>Microtus cf. pennsylvanicus</i> (Ord) (late Pleistocene)					
Clark's Cave, Virginia	2.02	1.75–2.33	.18	8.91	16
Strait Canyon Fissure, Virginia	1.78	1.5–2.1	.17	9.87	98
<i>Microtus chrotorrhinus</i> (Miller)					
St. Elzéar, Québec	2.00	1.68–2.39	.18	8.98	114
New Paris No. 4, Pennsylvania (late Pleistocene)	1.92	1.56–2.16	—	—	47
<i>Microtus xanthognathus</i> (Leach)					
Recent Alaska/Canada*	2.45	1.7–3.0	.37	15.06	30
Same as above (juveniles omitted)*	2.67	2.4–3.0		5.99	18
New Paris No. 4, Pennsylvania** (late Pleistocene)	3.40	2.7–4.0	.16 .23	6.68	100
Clark's Cave, Virginia (late Pleistocene)	2.40	2.00–2.80	.10	4.39	72

* Guilday and Bender, 1960.

** Guilday et al., 1964.

The coefficients of variation for length of both the anterior and posterior portions of M^3 are consistently higher than that of the total length of the same tooth (Table 6) because the delineation points of the latter measurement are precise, whereas the posterior limit of the third triangle that delineates AL from PL is often poorly defined, depending upon the degree of closure of the posterior portion of the third triangle.

The variable posterior portion of M^3 is usually shorter than the anterior portion. In *M. xanthognathus*, the species with the simplest M^3 , PL averages only 57.6% of AL; in *M. pennsylvanicus*, two Recent samples, it averaged 67% and 73%, and in one late Pleistocene sample, 69.5%. In *M. chrotorrhinus* PL is exceptionally well-developed, averaging 92% of AL in one Recent and one late Pleistocene sample, and in some individual cases, PL may exceed AL by as much as 32%. The differences can be correlated with the complexity of the occlusal pattern; the simpler the pattern, the shorter the relative length of the posterior portion (*M. xanthognathus*); the more complicated the pattern, the longer the relative length (*M. chrotorrhinus*).

An unexpected and interesting relationship is the inverse correlation between the degree of complexity of the posterior half of M^3 (as expressed by the mean of the length of the posterior portion divided by the mean of the length of the anterior portion) and its inherent vari-

Table 7.—Comparison of anterior and posterior length variability of M^3 , three species of *Microtus*. See text for length definitions.

Locality and measurements	Mean	OR	SD	CV	N	CV posterior	Mean posterior
						CV anterior	Mean anterior
<i>Microtus pennsylvanicus</i> (Ord)							
St. Elzéar, Québec							
Anterior length	1.09	.92–1.26	.09	8.55	57	1.363	.733
Posterior length	.80	.58–1.00	.09	11.66	58	—	—
Parramore Island, Virginia							
Anterior length	1.31	1.1–1.4	.097	7.37	50	1.451	.671
Posterior length	.88	.63–1.1	.094	10.7	50	—	—
<i>Microtus</i> cf. <i>pennsylvanicus</i> (Ord)							
Strait Canyon Fissure, Virginia (late Pleistocene)							
Anterior length	1.05	.90–1.3	.09	8.68	99	1.420	.695
Posterior length	.73	.60–.90	.09	12.32	97	—	—
<i>Microtus xanthognathus</i> (Leach)							
Clark's Cave, Virginia (late Pleistocene)							
Anterior length	1.51	1.35–1.75	.11	7.39	69	1.503	.576
Posterior length	.87	.55–1.05	.09	11.11	70	—	—
<i>Microtus chrotorrhinus</i> (Miller)							
St. Elzéar, Québec							
Anterior length	1.11	.92–1.34	.10	9.58	40	1.015	.927
Posterior length	1.03	.84–1.77	.10	9.70	40	—	—
New Paris No. 4, Pennsylvania (late Pleistocene)							
Anterior length	1.02	.80–1.12	.07	6.88	47	1.236	.921
Posterior length	.94	.72–1.20	.079	8.51	47	—	—

ability when compared to the more stable anterior half of M^3 (expressed as the coefficient of variation of the length of the posterior portion divided by the coefficient of variation of the length of the anterior portion, Table 8); as mean tooth complexity increases, the intrinsic variation of the posterior portion of the tooth apparently decreases, that is, variants tend to group more closely about their respective means.

The increased phenotypic variability of the posterior half of M^3 compared with the anterior portion suggests that it constitutes a more active evolutionary locus, but the apparent decrease in intrinsic variation with increasing dental complexity suggests that there may be a

Table 8.—Inverse correlation between degree of development and intrinsic variation between posterior portion (PL) and anterior portion (AL) of M^3 in three species of *Microtus*. See text discussion.

Taxon and locality	Mean PL	CV PL
	Mean AL	CV AL
<i>Microtus xanthognathus</i> (Leach)		
Clark's Cave, Virginia, late Pleistocene	.576	1.503
<i>Microtus pennsylvanicus</i> (Ord)		
Parramore Island, Virginia, Recent	.671	1.451
Strait Canyon, Virginia, late Pleistocene	.695	1.420
St. Elzéar, Québec, Recent	.733	1.363
<i>Microtus chrotorrhinus</i> (Miller)		
New Paris No. 4, Pennsylvania, late Pleistocene	.921	1.236
St. Elzéar, Québec, Recent	.927	1.015

point, probably dictated by jaw mechanics, beyond which evolution cannot proceed, given the present gene pool. Does this suggest that further development of M^3 in *M. chrotorrhinus*, the species with the most complicated M^3 , is approaching its functional limit of complexity given the mechanics of both upper and lower dental batteries? With the exception of the aberrant Guatemalan subgenus *Herpetomys*, *M. chrotorrhinus* has the most complex M^3 of any North American *Microtus*. Its dentition is apparently indistinguishable from *M. sachalinensis* Vasin (Gromov and Polyakov, 1977:293, Fig. 50) endemic on the island of Sakhalin, U.S.S.R, and a comparative morphological and ecological study of the two species might be worthwhile (Corbet, 1978). Dental evolution of the Microtini has been characterized by an increase in tooth complexity—the addition of cutting edges by increasing the number of transverse enamel ridges, one on the leading edge and one on the trailing edge of each new salient angle for more efficient propalinal mastication (Guthrie, 1965; Kesner, 1980; von Koenigswald, 1980).

This inverse correlation of tooth complexity and degree of variation suggests that, in species of *Microtus* with greater average tooth complexity, phenotypic possibilities become fewer as morpho-types eliminated from one end of the morphological spectrum are not compensated for by additions to the other, and the effective gene pool becomes progressively smaller. It is interesting to note that the species having the most complicated M^3 and showing at the same time the least amount of phenotypic variation, *M. chrotorrhinus*, is also the species with the most restricted habitat, suggesting a narrower niche width and stronger genetic selection. Van Valen (1965) proposed that a

species with broad ecological tolerance (such as, in this case, *M. pennsylvanicus*) might be expected to show a greater degree of genetic variation enabling it to cope with a more diverse environment than would a species in a more confining ecological niche and undergoing more rigid selection (here *M. chrotorrhinus*). He buttresses his argument with examples of birds drawn from mainland versus island habitats. Some species of birds, apparently released from competition, may occupy broader ecological niches on an island than on the adjacent mainland, but the opposite may also occur and much depends upon local circumstances (Van Valen, 1965; MacArthur, 1972). A correlation between niche-width and variation has not been convincingly demonstrated in mammals (Smith, 1981) and it appears not to apply in the present case as well (compare CVs, Table 6).

The fact that the correlation between increasing complexity and decreasing relative variation of the posterior portion of M^3 seems to pertain within as well as between the three species studied (*M. pennsylvanicus*, for example, Table 8) would seem to rule out the niche-width model in this instance. Nor does the correlation hold in overall length of M^3 versus relative variability of the posterior portion. The most plausible explanation, assuming that the phenomenon is biological and not a mathematical artifact that has escaped me, is that as the tooth approaches the limits of functional complexity, variation becomes progressively one-sided and the pattern becomes genetically "fixed."

OCCLUSAL PATTERN SUMMARY

Microtus xanthognathus (Leach).—Typical occlusal pattern of M^3 consists of anterior crescent, three alternating triangles, and a simple linguallly-directed posterior loop, a pattern shared by many other species of *Microtus* including *M. pennsylvanicus* (as in Fig. 2). There are typically three labial salient angles and three lingual cement-filled reentrant valleys. Compared with *M. pennsylvanicus* and *M. chrotorrhinus*, M^3 s of *M. xanthognathus* are conservative, showing less variation. The first and second alternating triangles were isolated from each other and showed no sign of fusion in 73 observations. Only 1.3% had a fourth lingual reentrant valley and only 12.3% showed any indication of an additional fourth labial salient angle. Because of their large size, about that of *M. richardsoni*, isolated M^3 s of adult *M. xanthognathus* can be easily distinguished from those of *M. pennsylvanicus* and *M. chrotorrhinus* by size alone (Table 6). Immature molars of *M. xanthognathus*, however, may be as much as 33.3% smaller than those of adult specimens, placing them well within the size range of the smaller species of *Microtus* (Guilday and Bender, 1960). The occlusal pattern, once established, does not change throughout the life

of the animal, so that there may be some difficulty in attempting to distinguish isolated M^3 s of young *M. xanthognathus* from those of large *M. pennsylvanicus* (but see Table 2, dealing with percentage differences in first and second triangle fusion).

The isolated M^3 s of *M. xanthognathus* from Clark's Cave were identified on the basis of their large size; small M^3 s were eliminated from consideration so that specimens could be confidently referred to *M. xanthognathus*. This is probably responsible for the low coefficient of variation of the total length of M^3 in the Clark's Cave *M. xanthognathus* sample (4.39 as against 8.98 *M. chrotorrhinus*, and 8.27 *M. pennsylvanicus*, Table 6). But, since the occlusal pattern of M^3 remains constant throughout the life of the vole, the elimination of juveniles from the *M. xanthognathus* sample will not bias the morphological picture.

M. xanthognathus, in addition to having the most conservative dental pattern, has the least relative development of the posterior portion of the tooth of any of the three species— $PL/AL = .57$ —although the degree of relative development is variable and overlaps with that of the other two species.

Microtus chrotorrhinus (Miller).—The M^3 of *M. chrotorrhinus* is the most complex of the three species studied (and of the subgenus). The anterior half of the tooth remains conservative but the posterior half is highly developed with a PL/AL ratio averaging .94, again with much variation and interspecific overlap. What was the anterior arm of the posterior loop in the other two species has the appearance, in *M. chrotorrhinus*, of an additional fourth and fifth triangle in various degrees of closure. The posterior arm of M^3 has developed an additional cement-filled (the 4th) lingual reentrant valley, present in 94.8% of the Quebec sample ($N = 155$) as opposed to only 1.3% ($N = 73$) in the *M. xanthognathus* Clark's Cave, Virginia, sample (Table 3). The fourth labial salient angle, present in only 12.3% of the Clark's Cave *M. xanthognathus* (Table 4) was well-developed in 100% ($N = 155$) of *M. chrotorrhinus* from Quebec. An additional fifth labial salient angle, not seen in either of the other two species, was noted in 21% of *M. chrotorrhinus*, and was weakly developed in an additional 7.7% (Table 4).

Microtus pennsylvanicus (Ord).—The occlusal pattern of M^3 in *Microtus pennsylvanicus* is highly variable. The basic pattern (as in *M. xanthognathus* and many other members of the subgenus) consists of an anterior crescent, three alternating triangles, and a lingually developed posterior loop. Variation may be so great that some individuals duplicate the complicated molar pattern of *M. chrotorrhinus*. Examples are illustrated by DeCoursey (1957:45, Fig. 8), Goin (1943:213, Fig. 1D), and this paper, Fig. 2C. The three species vary in percentage of M^3 s with isolated or fused first and second alternating triangles,

from 100% isolated in *M. xanthognathus* (Table 2) to from 91% to 95% fused in *M. chrotorrhinus*. Samples of *M. pennsylvanicus* M³s vary widely in degree of fusion, from a low of 9.8% (Quebec, N = 93) to a high of 43% (Comers Cave, Virginia, N = 132). During the initial stages of this study, during which only *M. chrotorrhinus* and *M. pennsylvanicus* M³s from Quebec were studied, it appeared that percentage of fusion of first and second alternating triangles was highly characteristic of each species. The discovery that 46.35% of all M³s from the late Pleistocene Strait Canyon, Virginia, site were also fused, associated with what appeared to be a high degree of incipient fourth lingual reentrant valley formation, led me to believe that the Strait Canyon sample represented a primitive stage in the evolution of *M. chrotorrhinus*. This was put to rest, however, when it was discovered that 43% of the Recent Comers Cave, Virginia, *M. pennsylvanicus* sample was fused as well, and that some degree of incipient fourth lingual reentrant valley formation was as common in Recent *M. pennsylvanicus* as in the Strait Canyon Pleistocene sample. Subsequent discoveries at Strait Canyon of upper maxillae of *M. pennsylvanicus*, which included the characteristic M²s, further heightened the assumption that the Strait Canyon sample of isolated M³s were indeed *M. cf. pennsylvanicus*. If isolated *M. chrotorrhinus* M³s were present in the sample, they must have been few and atypical.

DISCUSSION

The M³s of *Microtus* (of at least the subgenus *Microtus*) vary, both among samples drawn from single species and among species, in many characters; fusion or isolation of first and second alternating triangles, number and relative development of lingual reentrant valleys and labial salient angles, relative length and degree of variation of the occlusal pattern of the posterior portion of the tooth. Whether these characters vary geographically and temporally in meaningful patterns, remains to be seen. Unlike characters based upon soft anatomy, they have the advantage of being preserved in dated ancient materials, often in great quantity, and in Recent mammal collections, and their comparative study can serve as one means of investigating the evolutionary development of both past and present forms.

It has been demonstrated that isolated M³s of *M. pennsylvanicus*, *M. chrotorrhinus*, and *M. xanthognathus* cannot be relied upon for a specific identification in many cases; although each species has a morphological norm, individual variation overlaps species boundaries in all characters of M³s studied. If, however, large paleontological samples are available (such as the *M. cf. pennsylvanicus* sample from the early Wisconsinan Strait Canyon, Virginia, site), recourse to comparative statistical probabilities facilitates identification.

The M³ in the subgenus *Microtus* appears to be the most variable,

hence taxonomically useful, tooth and deserves further study to help elucidate patterns of evolution within and among the component species.

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SPECIMENS EXAMINED

() = number of skulls followed by number of M³s examined

- Microtus pennsylvanicus* (Ord) Recent: Caverne de St. Elzéar de Bonaventure, Québec, Canada (LaSalle & Guilday, 1980), CM 30419, 30420, 30427–30432, 30434 (93); Comers Cave,* Page County, Virginia (91–132), G-865; New Paris No. 3, Bedford County, Pennsylvania, G-910, (11–20); Parramore Island,* Accomack County, Virginia, Merritt Collection uncatalogued (501–1001). Late Pleistocene: Clark's Cave, Bath County, Virginia (Guilday et al., 1977). CM 24521 (17); Connecticut, Recent: UCM 2570.
- Microtus* cf. *pennsylvanicus* (Ord) late Pleistocene: Strait Canyon fissure, Highland County, Virginia. CM 38496–38524 (153).
- Microtus breweri* (Baird) Recent: Muskeget Island, Massachusetts. BU 1059, 1061, 1070, 1073, 1075, 1079.
- Microtus chrotorrhinus* (Miller) Recent: Caverne de St. Elzéar de Bonaventure, Québec, Canada. CM 30384, 30400, 30404, 38514–38523 (155). Late Pleistocene: New Paris Sinkhole No. 4, Bedford County, Pennsylvania (Guilday et al., 1964). CM 5595, 5597, 5598, 5611, 5612, 5684, 6096, 8184, 8185, 8186, 6210, 6288, 6289, 6290, 6307, 6313, 6722a,b,c, 6766, 6767, 6854, 6855, 6863, 6924, 6929, 7241, 7242, 7385, 7715, 7784a,b, 7414 (49).
- Microtus xanthognathus* (Leach) Late Pleistocene: Clark's Cave, Bath County, Virginia. CM 24572 (88); New Paris Sinkhole No. 4, Bedford County, Pennsylvania. CM 5553–5557, 5559, 5562, 5578, 5911, 6182, 6251, 6252, 6295, 6301, 6733, 6747, 6753, 6764, 6841, 6868, 6870, 6894, 7153, 7167, 7169, 7172, 7196–7199, 7200–7207, 7209, 7210, 7212–7219, 7222, 7226, 7387, 7412, 7415, 7636, 7638–7640, 7647, 7648, 7650, 7651, 7670, 7679, 7680, 7683, 7685–7687, 7695–7698, 7720, 7765 (119).

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FOSSIL SMALL MAMMALS FROM THE KECHABTA FORMATION, NORTHWESTERN TUNISIA

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ABSTRACT

Small collections of fossil mammals from several localities in the Kechabta Formation of northwestern Tunisia contain insectivores, lagomorphs, and rodents. These taxa support a late Vallesian to mid-Turolian age for the Kechabta Formation. One new species of Cricetidae, *Zramys jaegeri*, is described.

INTRODUCTION

Since 1967, the University of Colorado Museum has coordinated a multinational program to collect and study the fossil vertebrates from the Neogene rocks of Tunisia. The earlier part of the program concentrated on the larger vertebrates from the Beglia Formation (Middle Miocene) of central Tunisia. Since 1971, fossil smaller vertebrates of Middle and Late Miocene age and some of Pliocene age have been collected from a number of sites in northern Tunisia. The oldest of these localities is in the Middle Miocene part of the Hakima Formation

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(Robinson and Black, 1973). The purpose of the present paper is to describe the fossil smaller mammals from the Upper Miocene Kechabta Formation in the area from Jendouba (Souk el Arba) to south of El Kef, northwestern Tunisia. Comments on fossils from the Hakima Formation supplement an earlier paper (Robinson and Black, 1973). The geology and Cricetidae are reported by Robinson, the Muridae and Sciuridae by Black, the Erinaceidae and Soricidae by Krishtalka, and the Ochotonidae by Dawson. These fossils help to date the Hakima and Kechabta Formations, complement Jaeger's (1977*b*) study of Maghreb Miocene rodents, and add information on the smaller mammals of the Middle and Late Miocene of the Maghreb. Collections from the younger Mellegue Group in northern Tunisia will be described later.

ABBREVIATIONS

T-, 0000 field numbers of specimens in the SGT; L, length; W, width; SGT—Service Géologique de Tunisie; UCM—University of Colorado Museum; CM—Carnegie Museum of Natural History. (All measurements are in millimeters.)

GEOLOGIC SETTING

The post-Burdigalian continental deposits of Tunisia north of the Dorsale are found in a number of more or less isolated basins related to tectonically complex situations. The numerous diapirs of the region have been active for a long time; very few of the outcrops are not involved in this diapirism. Biely et al. (1974) established a stratigraphic framework for the region based in part on the work of Buroillet (1951). They proposed that the lower sequence be called the Medjerda Group including, from base to top, the Hakima, Oued Melah, Kechabta, and Oued bel Khedim Formations of Buroillet (1951). This group is predominantly continental in origin and often contains very coarse conglomerates. Brackish water beds may occur in the Oued bel Khedim and Oued Melah Formations, especially in the northeast. They also proposed the Mellegue Group, containing the Tessa (lower) and Oued Djouama (upper) Formations; where contacts are visible, the Mellegue Group unconformably overlies the Medjerda Group. The only localities where these contacts are not angular and can be observed are at Araguib Kammra, southeast of El Kef (Buroillet, 1956), and in the valley of the Oued Mellegue, south of Jendouba.

Correlation of the deposits in the El Kef-Jendouba area with those of the type sections of the Hakima-Kechabta Formations south of Bizerte is difficult; however, the superb section at the Araguib Kammra cited by Buroillet (1956) resembles the latter. Fossils have been recovered from all of these formations.

PREVIOUS WORK

The first Neogene locality in northern Tunisia that produced a fossil vertebrate fauna was Lac Ichkeul (Arambourg and Arnould, 1949; Jaeger, 1971; Coppens, 1971), where both large and small mammals were collected. This locality is possibly in the Oued Djouama Formation. Undescribed material subsequently collected includes: a jaw of a juvenile individual of *Hipparion* sp. from the Hakima Formation near Ben Mtir dam, north of Jendouba; a complete skull of *Hipparion* sp. from the Oued Melah Formation southeast of Mateur at Kef en Nsoura; and two *Hipparion* teeth from near the base of the Kechabta Formation at Oued Mellegue (Biely et al., 1974). All of this material is in the collections of the SGT.

Described material subsequently collected includes: mastodont and rodent remains from Djebel Semmene in the Kechabta Formation northeast of Jendouba (Jaeger, 1977b; Bergounioux and Crouzel, 1956); a small collection from the Hakima Formation near Testour (Robinson and Black, 1973). The results of this previous work indicated that the Hakima Formation was late Astaracian to Vallesian, the Kechabta, Vallesian and Turolian, and the Djouama, at least in part, Villafranchian.

NEW LOCALITIES

New localities found since 1971 are:

Hakima Formation.—At Testour, slightly higher in the section than the locality reported by Robinson and Black (1973).

Kechabta Formation.—1) Voie Ferrée: on the west bank of the Oued Mellegue, some 12 km south of Jendouba near the top of the formation (40 m west of an abandoned railway bed). 2) MDM locality, Zag et Tir: an exposure southwest of El Kef near the Marabout of Sidi Ounis, near the section cited by Burollet (1956), and slightly below the freshwater limestones at the top of the section. 3) Araguib Kammra: in a ravine exposed west of the El Kef-Sbeitla road, 9–10 km southeast of El Kef. This section, about 4 km west of that cited by Burollet (1956), contains several localities, including one near the contact of the Kechabta and the Oued bel Khedim Formations.

Tessa Formation.—1) Koudiat er Rouabi: 34 km east of El Kef and 1.5 km north of the road. Two levels are productive here: one is approximately 50 m above the base of the exposures that have a faulted lower contact; the second level was 10–12 m above the first, but has been destroyed by recent construction. 2) Calcaires Lacustres: 33 km east of El Kef and 5 km south of the road. The productive bed is a dark organic shale in a sequence containing freshwater limestones. It is 45–50 m above the contact with folded Eocene limestones. 3) An

exposure on the top of a hill, 5 km south of Hammam Biada, and east of Oued Tessa.

AGE OF THE HAKIMA FORMATION

The first vertebrate specimen from the Testour localities in the Hakima Formation was discovered in samples being sorted for foraminifera. More intensive collecting produced the faunule described by Robinson and Black (1973). These deposits were thought to represent a sequence of continuous marine sedimentation from the Oligocene to the Late Miocene (Bajanik and Salaj, 1971), even though such a sequence had never been found in northern Africa, a region where the Burdigalian marine sediments lie unconformably upon older sediments. Robinson and Black (1974) accepted the foraminiferal evidence. Their 1974 paper was prepared for and presented at the 75th anniversary meeting of the Egyptian Geological Survey in 1971. Later, Robinson and Black (1973) considered the foraminifera to have been reworked and that the mammalian fauna indicated a true late Miocene age. Recent field work by Professor M. B. Cita of the University of Milan has confirmed (written communication to Robinson, 1976) the reworked nature of the sediments; the mammalian fauna definitely indicates a late Astaracian (middle Serravallian) age for these deposits, not an Aquitanian or Burdigalian one.

The four beds in the Hakima Formation, Testour area, that produced bone were designated localities 00, 0, 1, 2, from oldest to youngest. The fauna from one of these, locality 00, has been described (Robinson and Black, 1973). Localities 0-2 occur in one section on the north side of Djebel Ras el Krab, in a location where the base of the Hakima Formation is in fault contact with a diapir of Triassic rock. At locality 00, about 1 km to the west of localities 0-2, the same diapir does not intersect the Hakima Formation, but is in fault contact with the upper (continental) part of the Oligocene Fortuna Sandstone; here the Hakima Formation overlies the Fortuna Sandstone unconformably. Locality 00 is some 5 m above the contact with the Fortuna Sandstone. Although stratigraphically higher, the exact positions of localities 0-2 relative to 00 cannot be determined; there are no discernable differences among the taxa from these localities.

LOCALITIES IN THE KECHABTA FORMATION

The Kechabta Formation is extensively exposed from southeast of Bizerte (type section at Djebel Kechabta, Burrollet, 1951) to west of the Algerian frontier. It is usually in tectonically complex situations due to the numerous diapirs in the region and to at least two phases of post-Kechabta orogeny. The sections at the Oued Mellegue, Testour, and Araguib Kammra preserve the stratigraphic relationships of

the Kechabta to the underlying Hakima Formation. At the Araguib Kammra, the upper shale unit of the Medjerda Group, the Oued bel Khedim Formation, is preserved (Burolet, 1956). At this exposure, the unconformity between the Medjerda and Mellegue groups is less pronounced than elsewhere. The locality of Voie Ferrée, at Oued Mellegue, is near the top of the preserved Kechabta sequence, but the overlying Tessa Formation rests upon the Kechabta with a pronounced angular unconformity indicating significant erosion of the Kechabta prior to deposition of the Tessa Formation.

SYSTEMATIC ACCOUNTS

Order Insectivora Illiger, 1811

Family Erinaceidae Fischer von Waldheim, 1817

Schizogalerix Engesser, 1980

Schizogalerix moedlingensis (Rabeder), 1973

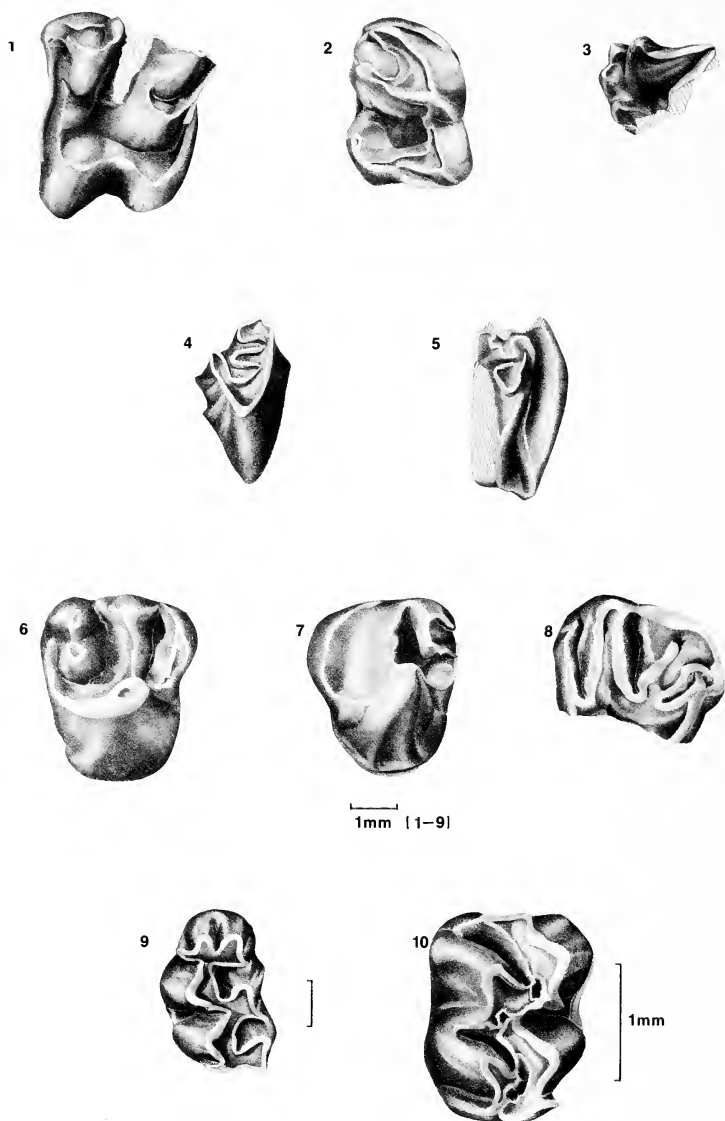
Schizogalerix ?moedlingensis

Figs. 1, 2

Referred specimens.—T-4421, isolated left M¹; T-4417, fragment of right dentary with M₂, roots of M₃; T-4423, isolated left M₂.

Locality.—UCM locality 77290, MDM locality, Zag et Tir: Turolian.

Description.—The posterolabial border is broken away from the isolated M¹ (L = 2.6+; W = 3.4). The crown is quadrate in occlusal view with essentially straight anterior and posterior margins and a deep lingual emargination. The M¹ bears six major cusps aligned labiolingually in two high, parallel rows; the protocone, paraconule, and hypocone form the anterior row; the hypocone, metaconule, and metacone, the posterior one. In occlusal view, the apices of the paraconule and metaconule are anterior, respectively, to imaginary lines connecting the apices of the protocone and paracone, and the metacone and hypocone. A deep valley separates the two rows of cusps and extends lingually from the buccal border of the crown to a high crest that unites the protocone and hypocone. Apart from the paraconule, all of the major cusps are subcrescentic, with high convex lingual faces and concave labial ones, so that their apices point buccally. The protocone, the largest of the cusps, occupies the anterolingual corner of the crown. The preprotocrista is short, parallel to the anterior margin of the tooth, and extends to the small, low, pyramidal paraconule. The postprotocrista runs posteriorly and joins the prehypocrista to form a high crest that demarcates the lingual and occlusal surfaces of the crown. The base of the protocone extends farther lingually than that of the hypocone, creating a deep emargination between the two cusps on the lingual surface of the crown. The hypocone is lower and less compressed anteroposteriorly than the protocone. A small cuspule occurs between the two cusps at the junction of the prehypocrista and postprotocrista. The posthypocrista runs labially for a short distance and ends at the base of the crown at a point directly posterior to the metaconule. The latter, about four times as large as the paraconule, is higher than the hypocone, but lower than the metacone. The premetaconulecrista is short, but the longer postmetaconulecrista runs posterolabially to form a broad metacingulum along the posterior wall of the metacone. The latter is the highest cusp on the crown. The premetacrista is short and appears to become thicker (?mesostyle) at its broken labial edge. The paracone also bears a short preparacrista and a longer postparacrista that ends in a large mesostyle. Importantly, the latter is not connected posteriorly to any crests. If, as it appears, two mesostyles were present,



Figs. 1, 2.—*Schizogalerix ?moedlingensis*. 1) T-4421, left M^1 . 2) T-4417, right M_2 .
 Fig. 3.—*Soricidae* indet. T-4312, left P^4 .
 Figs. 4, 5.—*Prolagus* sp. 4) T-3807, P^2 . 5) T-3806, P^4 .
 Figs. 6–8.—*Atlantoxerus* sp. 6) T-4403, right M^1 or M^2 . 7) T-4344, left P^4 . 8) T-4313, left M^1 or M^2 .
 Figs. 9, 10.—*Zramys jaegeri*, new species. 9) T-4419, left M^1 , holotype. 10) T-4407, right M^2 .

they would have been completely separate on an unbroken M^1 . A low conical parastyle occurs directly anterior to the apex of the paracone, and is separated by a notch from the preparamacrista. The precingulum is strong and runs lingually from the parastyle to the anterior part of the base of the protocone. The postcingulum is short and weak, as is the parastylar ectocingulum.

T-4417 is a jaw fragment with a slightly worn M_2 ($L = 2.5$; $W = 2.0$) and the roots of a much smaller M_3 . T-4423, another M_2 ($L = 2.6$; $W = 2.2$), is highly worn. The lower molars lean lingually, so that the labial face of the crown is long and sloping. The trigonid and talonid are equal in length, but the latter extends farther buccally than the trigonid. In occlusal view, the crown of M_2 is essentially rectangular, except for the anterolingual orientation of the anterior face of the trigonid. The posterior wall of the trigonid is also oriented anterolingually, so that the metaconid occurs more anteriorly, relative to the protoconid. The paraconid, an elongate cusp, is connected to the protoconid by a broadly worn paracristid, but is isolated from the higher, conical metaconid. The anterior cingulid is strong, but does not extend onto the buccal surface of the crown. The talonid bears two main cusps—a broad, low hypoconid, and a higher entoconid that is laterally compressed and drawn out toward the metaconid. As is typical of erinaceids, the cristid obliqua meets the trigonid wall labially, below the worn apex of the protoconid, and is parallel to the long axis of the tooth. As a result, the hypoflexid notch is very shallow. On the opposite side of the crown, a small notch separates the bases of the metaconid and entoconid, and, in lingual view, this notch is at the same height as that between the paraconid and metaconid. The posterior border of the talonid is parallel to that of the trigonid, and shows no evidence of a hypoconulid. Rather, two crests meet at the midpoint of the posterior margin of the talonid basin: a short hypocristid and a longer postcingulid that runs obliquely from the tip of the entoconid to the posterolabial part of the base of the talonid.

Discussion.—*Schizogalerix*, a new genus of echinosoricine erinaceid, was named by Engesser (1980) for a number of new species from the Miocene of Turkey and North Africa, as well as some formerly included in *Galerix* [*S. moedlingensis*, *S. voesendorfensis*, *S. zapfei* (including *S. attica*)]. Species that Engesser (1980) retained in *Galerix* are the generotype, *G. exilis*, and *G. socialis*. Accordingly, the insectivore material recently described from the Turolian of Samos (Black et al., 1980) belongs to *S. zapfei* (= *S. attica*) rather than *G. atticus*.

Among the characters preserved on the three molars described here, *Schizogalerix* differs from *Galerix*, according to Engesser (1980), in the presence of a divided mesostyle and an isolated metaconule on M^1 , and, on M_2 , in the tendency to develop a "free-ended" hypocristid. Some of these features may not, however, be consistently diagnostic. Upper molars of *Galerix socialis* (Engesser, 1972:45, Fig. 1; 48, Fig. 3) also have an isolated metaconule and the lower molars (Engesser, 1972:46, Fig. 2) do not differ from those of many species assigned to *Schizogalerix* (Engesser, 1980:64, Fig. 3) in the structure of the hypocristid-postcingulid complex.

The M^1 described here appears to have had the divided mesostyle characteristic of *Schizogalerix*. The M_2 s are referred to the same taxon as the M^1 on the basis of association and similar size. All three teeth most closely resemble comparable parts of the dentition of *S. moed-*

lingensis, among described species of that genus—the anterior mesostyle on M^1 appears to have been completely separated from the premetacrista and, if present, the posterior mesostyle; the hypocristid-postcingulid junction is medial and strong (Engesser, 1980:74, Fig. 11). However, referral of these teeth to *S. moedlingensis* is tentative, because of the small sample size, the missing and potentially diagnostic metastylar area of M^1 , and the variable occurrence of some of the above mentioned features in material assigned to *S. aff. voesendorfsensis* and a number of new species of *Schizogalerix* (Engesser, 1980: Figs. 3a, 3e, 4c, 10, 14, 19c). The size of the teeth is also not helpful taxonomically. According to Engesser's (1980:71,72) data, described species of *Schizogalerix* have closely overlapping ranges of variation in size of M^1 and M_2 . The material discussed here is slightly larger than M^1 and M_2 of these species, and, if it does belong to *S. moedlingensis*, would increase the known range of variation in size of M^1 and M_2 of that species.

S. moedlingensis is otherwise known only from Eichkogel, an Austrian locality of late early Turolian age (Engesser, 1980).

Family Soricidae Gray, 1821

Soricid indet.

Fig. 3

Referred specimen.—T-4312, isolated left P^4 .

Locality.—Voie Ferrée; Turolian

Description.—This fragmentary P^4 ($L = 1.7$; $W = 1.7+$) is missing the hypoconal shelf (posterolingual corner of the crown). The labial part of the crown is dominated by a high, conical paracone and a slightly lower crest that extends from the latter to the posterolabial tip of the crown. A strong lip of enamel runs lingually from this point and forms the posterior margin of the occlusal surface of the premolar. Curiously, a wide flange of enamel, of which the posterior margin is broken, extends posteriorly from the base of the crown along the entire preserved posterior margin of the tooth. This flange does not appear to have been part of the occlusal surface, but may have filled the interdental embrasure between P^4 and M^1 . The preserved part of the lingual half of the crown bears a small protocone and hypocone, both of which occur on the anterior margin of the tooth. The protocone is very close to the small parastyle, whereas the hypocone is more lingual. The labiolingual orientation of the preserved part of the posterior margin of the hypoconal shelf implies that the posterior emargination in this area was only slight.

Discussion.—This isolated and fragmentary P^4 cannot be identified to subfamilial, much less generic, level. The proximity of the protocone to the parastyle and the slight posterior emargination are features that occur in a number of crocidurines and soricines.

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Prolagus Pomel, 1853

Prolagus sp.

Figs. 4, 5

Referred specimens.—T-3806, P⁴; T-3807, P² (L = 1.0; W = 1.6); T-4240, P₃ (L = 1.7; W = 1.9).

Locality.—Voie Ferrée; Turolian.

Discussion.—The three teeth are referable to a species of *Prolagus*, but the sample is too small to permit reference to any of the notably variable species of this genus. P² (Fig. 4) is a relatively advanced tooth with short external and medial lobes and a long internal lobe that extends buccally in front of the medial lobe. The tooth is thus more advanced than in *P. oeningensis* and resembles that of *P. michauxi* (Lopez-Martinez and Thaler, 1975) and some variants from Polgardi (Tobien, 1963), Kohfidisch (Bachmeyer and Wilson, 1970), and Pikerimi (Lopez-Martinez, 1976). P⁴, a broken specimen (Fig. 5) has traces of two buccal lakes. P₃ has the structure typical of *Prolagus* and lacks a crochet. This is the earliest record of *Prolagus* in Africa, predating the Villafranchian occurrences in Algeria and Tunisia (Michaux, 1975; Jaeger, 1971) and marking a break from the earlier faunas in which the lagomorphs are represented by *Kenyalagomys* and its allies.

Order Rodentia Bowdich, 1821
Family Sciuridae Gray, 1821
Genus *Atlantoxerus* Major, 1893

Atlantoxerus sp.

Figs. 6, 7, 8

Referred specimens.—T-4344, LP⁴ (L = 2.37, W = 2.80); T-4313, LM¹ or M² (W = 2.80); T-4403, RM¹ or M² (L = 2.37, W = 3.00).

Localities.—Voie Ferrée (T-4344); Araguib Kammra B (T-4313); MDM locality, Zag et Tir (T-4403). All Turolian.

Description.—P⁴ has a wide anterior cingulum, with a high parastyle. The protoloph is a high, thin crest with only a slight wrinkle at the posterior margin of the protoconule. The metaconule is isolated from the protocone and has a thin crest passing posteroanteriorly a short way along the posterior margin of the tooth.

The upper molars display rather narrow anterior basins with moderate parastyles. The protoloph is narrow, without protoconules. The metalophs are short, terminate in large metaconules, and are separate from the protocones except in a very advanced stage of wear. The posterior arm of the protocone ends behind the metaloph between the metacone and metaconule.

Discussion.—The three specimens are clearly those of *Atlantoxerus* but the material is much too fragmentary for a specific assignment.

Table 1.—Measurements (in mm) of undamaged specimens of *Zramys jaegeri*.

T. no.	Tooth	Length	Width
4419	M ¹	2.50	1.68
4418	M ¹	2.62	1.81
4415	M ¹	2.92	1.84
4414	M ²	2.00	1.45
4407	M ²	1.95	1.57
4410	M ³	1.35	1.45
4406	M ₁	2.40	1.52
4405	M ₁	2.47	1.48
4408	M ₂	1.92	1.49
4413	M ₂	2.08	1.62
4424	M ₂	2.00	1.50
4422	M ₂	2.21	1.65

Family Cricetidae Rochbrunne, 1883

Subfamily Uncertain

Genus *Zramys* Jaeger and Michaux, 1973, in Jaeger et al., 1973*Zramys jaegeri*, new species

Figs. 9, 10; Table 1

Holotype.—T-4419, M¹.*Hypodigm*.—T-4420, M¹–M² eroded; T-4419 (holotype), 4418, 4415, M¹; T-4407, 4411, 4412, 4414, M²; T-4410, M³; T-4405, 4406, 4416, M₁; T-4404, 4408, 4413, 4414, 4422, M₂.*Locality*.—UCM Locality 77290; MDM Locality, near Sidi Ounis, Zag et Tir, southwest of El Kef, Tunisia. Turolian.*Diagnosis*.—Size of *Z. dubius* and *Z. semmemensis*; M₁ with well developed posterior ectoloph, anterocone deeply cleft and usually with anterobuccal and anterolingual spurs directed laterally but not as extreme as in *Z. haichai*; posterior ectoloph at buccal margin of tooth not forming partial spur ending lingual to the buccal margin as in *Z. semmemensis* and *Z. haichai*.*Description*.—Although teeth other than M¹ are known, only the M¹ of *Z. semmemensis* was figured by Jaeger (1977b); no other comparative material is described in the literature. *Z. jaegeri* is more hypsodont than *Z. semmemensis* and the closure of the posterior fold (terminology of Van de Weerd, 1976) indicates a more derived condition than in the species from Djebel Semmene. One specimen (T-4418) is lacking the anterolingual spur but has the well developed posterior ectoloph and anterobuccal spur.*Discussion*.—There is confusion about the subfamilial status of *Zramys*. Jaeger (1977b) placed it in "subfamily indet." (p. 87), but suggested (p. 109) that it is closely related to *Mellalomys atlasi*, which he (1977a, 1977b) placed in the Myocricetodontinae. He also stated that *Zramys* may have given rise to a form from Lac Ichkeul which resem-

bles *Ruscinomys*. Lavocat (1961) did not include *Cricetodon atlasi* (now *Mellalomys atlasi*) within the Myocricetodontinae, but compared it to *Cricetodon gregarius hispanicus*. *Cricetodon gregarius* has now been made the type of a new genus, *Megacricetodon*, and the subspecies *hispanicus* has been elevated to a species of *Megacricetodon* (Mein and Freudenthal, 1971).

One of the important characteristics of the tribe Cricetodontini is the presence of four to five roots on the M^1 , whereas the Megacricetodontini, *Zramys*, and *Mellalomys*, all have three. One of the characteristics of the Myocricetodontinae (if *Mellalomys* is excluded) is the presence of a prominent accessory lingual cusp on M^1 . Although Jaeger's (1977b) classification is followed here, more detailed studies may support including the *Mellalomys-Zramys* group within an uncertain tribe of the Cricetodontinae. *Megacricetodon* often has a spur (eperon) behind the paracone of M^1 as does *Zramys* (Mein and Freudenthal, 1971:23).

De Bruijn (1976) and Tobien (1978) placed *Byzantinia* and *Turkomys* in the tribe Cricetodontini. Although the number of the roots of M^1 of these genera is not given by Tobien, two specimens of *Byzantinia hellenicus*, CM-36258 and CM-36260, each have four roots. If this character is constant, the *Turkomys-Byzantinia* lineage is more closely related to *Hispanomys-Ruscinomys* than either is to the *Mellalomys-Zramys* group.

In the *Hispanomys-Ruscinomys* lineage, there is a gradual development of hypsodonty, a tendency for the completion of the ectoloph, and a simplification of pattern (Van de Weerd, 1976). These genera do not have a lingual anterolophule spur on M^1 . In the *Turkomys-Byzantinia* lineage the anterolophule spur becomes well developed (Freudenthal, 1970: Fig. 1; De Bruijn, 1976: pl. 1, Fig. 5, 8; Tobien, 1978: Fig. 10; Black et al., 1980: Fig. 7c). The presence of an anterolophule spur and a complete ectoloph in *Hispanomys sofcaensis* (Tobien, 1978), suggest that it should probably be placed in *Byzantinia* (as Unay, 1980:402, has done). The position of *H. eskihisarensis* is problematical as it lacks the anterolophule spur but has an elongate M^3 characteristic of *Turkomys-Byzantinia*. In *Turkomys pasalarensis* and *T. candirensis* the spur is weak, and perhaps some individuals did not develop it. Unay's (1980) discussion of the diverse *Byzantinia* material from Bayraktepe helps to fill in details of the lineage.

In *Zramys*, a functionally similar but not homologous crest is present in some species, including the type, *Z. haichai* (Jaeger, 1977b: pl. 4, Fig. 1, 2). This crest, here termed the anterolingual spur, projects from the posterior part of the lingual portion of the anterocone, and may be accompanied by an anterobuccal spur on the buccal portion of the anterocone. In *Zramys*, the development of the ectoloph is not as

pronounced as in either *Ruscinomys* or *Byzantinia*. However, in *Zramys*, there is no tendency for the simplification of pattern found in *Ruscinomys*. The complex pattern of the M^1 of *Zramys* is matched by the M_1 (Jaeger, 1977b: pl. 4, Fig. 5), which is much more complex than M_1 of *Byzantinia* (Black et al., 1980: Fig. 7a) or *Ruscinomys* (Van de Weerd, 1976: pl. 13, Fig. 1).

The *Hispanomys-Ruscinomys* lineage seems to have been restricted to southwest Europe (with the possible exception of *H. eskihisarensis*, although Unay, 1980, may be right in placing this species in *Byzantinia*), the *Turkomys-Byzantinia* lineage to southeast Europe and Anatolia, and *Zramys* to northwest Africa (De Bruijn, 1976:367). Throughout the Middle and Late Miocene there appear to have been at least three centers of cricetodontine evolution in which a general tendency for hypsodonty, marked bilobation of the anterocone of M^1 and development of an ectoloph occurred. The hypsodonty became extreme in Ruscinian *Ruscinomys*; Ruscinian *Zramys* and *Byzantinia* are not known.

Subfamily Myocricetodontinae Lavocat, 1961

Genus *Myocricetodon* Lavocat, 1961

Myocricetodon seboui Jaeger, 1977b

Myocricetodon sp. cf. *M. seboui*

Referred specimen.—T-4396. Left M^1 , missing anterocone.

Locality.—Araguib Kammra C, approximately 50 m below AK-B and approximately 60 m below the contact with the Oued bel Khedim Formation. Turolian or latest Vallesian.

Discussion.—This is the only known cricetid specimen from the Araguib Kammra. The lack of the anterocone makes certain identification doubtful, but the M^1 possesses the cusp behind the protocone typical of most *Myocricetodon*; the width of M^1 , 0.85 mm, is well within the range of size given by Jaeger (1977b) for *M. seboui* from Oued Zra. The geologic record of *M. seboui*, according to Jaeger (1977b), extends from middle Vallesian to late early or early middle Turolian. The specimens that Jaeger (1977b) reported from Djebel Semmene (*M.* sp. cf. *M. seboui*) were all larger than the sample of *M. seboui* from Oued Zra, as were those from Amama 2. The Araguib Kammra specimen is closest in size to M^1 of *M. seboui* from Oued Zra (late Vallesian).

Family Muridae Gray, 1821

There are two species of murids represented in the collections from the Kechabta Formation of north central Tunisia. These are of Turolian age and possibly contemporaneous with species from Amama 2 (Algeria) and Khendek el Ouaich (Morocco) (Jaeger, 1975).

Table 2.—Measurements (in mm) of cheek teeth of species of *Anthracomys*.

Species	M ¹		M ²		M ₁	
	L	W	L	W	L	W
<i>Anthracomys majori</i> (Michaux, 1971)	3.40	2.10	1.90	2.10	2.80	1.90
<i>Anthracomys filfilae</i> (Petter, 1968)	—	—	—	—	3.00	2.00
<i>Anthracomys meini</i> (Michaux, 1969)	2.42	1.65	—	—	2.12	1.34
<i>Anthracomys anomalus</i> (De Bruijn et al., 1970)	2.19	1.57	1.57	1.54	2.08	1.36
<i>Anthracomys miocaenicus</i> (Jaeger, 1975)	2.32	1.57	1.47	—	2.08	1.35
<i>Anthracomys</i> species A	2.10	1.40	1.40	1.35	—	—
<i>Anthracomys</i> species B	2.80 ^a	2.15 ^a	2.10	2.00	2.50	1.60

^a M¹ broken, measurement approximate.

Older murids are known from North Africa, with *Progonomys* cf. *P. cathalai* from Bou-Hanifia II (Jaeger et al., 1973) being the oldest known to date. The specimens from the Kechabta Formation are fragmentary and few in number, but appear to represent species more advanced than *Progonomys cathalai*. They are quite probably referable to the genus *Anthracomys* (Petter, 1968; Jaeger, 1975), showing some resemblance to *Anthracomys majori* as characterized by Missonne (1969:83) and *Anthracomys miocaenicus* (Jaeger, 1975). Indeed, it is difficult to separate *Anthracomys* (Michaux, 1969:14) from *Paraethomys* (Jaeger, 1975:87). In both, stephanodonty is said to be moderately developed; the posterior cingulum (Z) is very reduced or absent on the upper and lower first molars; there is no anterior cusp (Sm) on M₁ and the cingular cusps of M₁ are reduced. In the original description of *Paraethomys filfilae* (Petter, 1968) the only comparisons made to a fossil murid were to the strongly stephanodont *Stephanomys donnezani*. In other discussions of both *Paraethomys* and *Anthracomys* (see Michaux, 1969; Missonne, 1969; Jaeger, 1971, 1975) no comparisons between the two genera are made. It would seem that these two genera are congeneric, with *Anthracomys* having priority. Valid species would include:

Anthracomys majori (Schaub) 1938

Anthracomys filfilae (Petter) 1968

Anthracomys meini (Michaux) 1969

Anthracomys anomalus (De Bruijn et al.) 1970

Anthracomys miocaenicus (Jaeger et al.) 1975

We would exclude *A. ellenbergeri* from this genus, following Michaux (1969:11), who established the genus *Valerymys* for this species.

The Tunisian specimens are not sufficiently complete to warrant the naming of new taxa, and they are not assignable to any known species of *Anthracomys*. Two species are present, one (*Anthracomys* sp. B) considerably larger than the other (*Anthracomys* sp. A), but otherwise quite similar in occlusal morphology.

Anthracomys Schaub, 1938

Anthracomys sp. A

Figs. 11, 12; Table 2

Referred specimens.—T-4080, RM¹; T-3808, RM¹; T-4212, RM₂.

Locality.—Voie Ferrée; Turolian.

Description.—The enamel has been lost along the labial cusps and on T2 of M¹. T1 is set well back of T2 with its anterior border in line with the posterior border of T3. T1 and T4 are of equal size and there is a well defined though narrow crest from T1 to T4. A crest was probably also present from T3 to T6. T4 and T6 lie behind T5. There is no T7 and T9 is small. The stephanodont crest T4 to T8 and T6 to T9 are present. There are no cingular cusps on M¹, and Z, if present was quite small. M² has T1 much larger than T3 and set further posteriorly than T3. There are no crests from T1 to T4 or T3 to T6. Crests from T4 to T8 and T6 to T9 are prominent. Z is very small.

Anthracomys sp. B

Figs. 13-16; Table 2

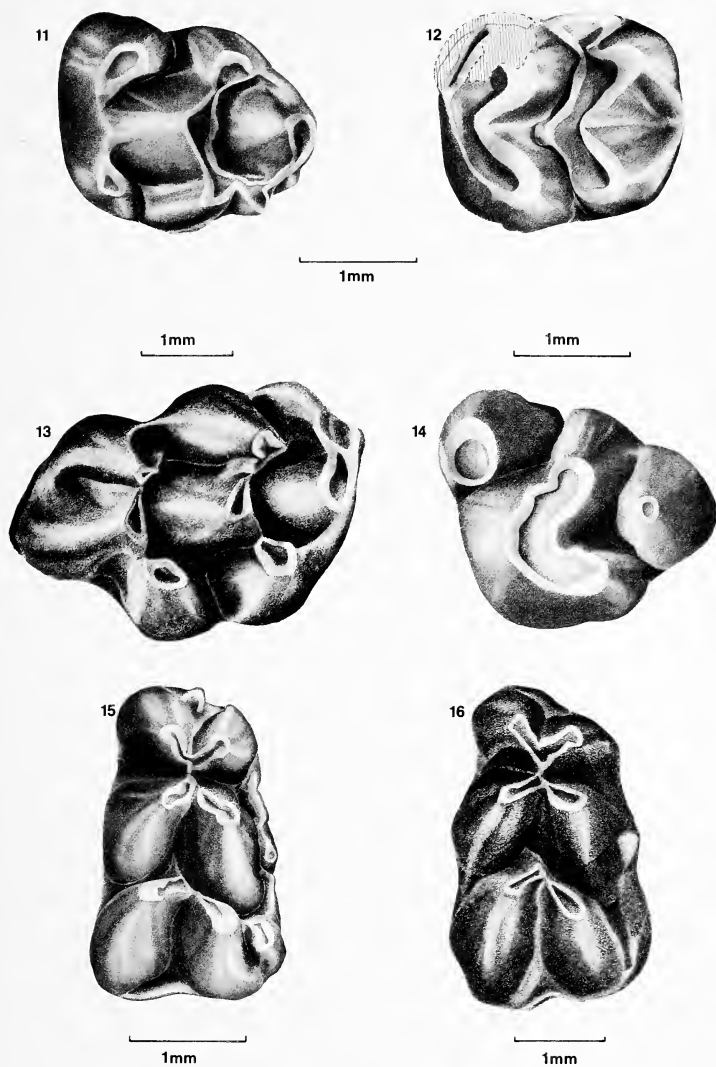
Referred specimens.—UCM-34887, RM¹–RM³; T-4211, LM¹; UCM-34886, RM²; T-4242, LM³; T-4210, RM₁; T-4241, RM₁; UCM-34888, LM₁; T-4208, LM₂.

Locality.—Voie Ferrée; Turolian

Description.—The maxillary fragment with M¹–M³ is badly cracked as are the teeth. The cusps on the upper molars are large and rounded. There does not appear to be any overlap of M² by M¹. T1 is set behind T3 but not as markedly as in the smaller form. There are no T1 to T4 or T3 to T6 crests, but there are thin crests from T4 to T8 and T6 to T9. T9 is much larger than it is in the smaller *Anthracomys* sp. A. Z is present on M¹ as a small spur off the posterolabial corner to T8. On M², T1 is much larger than T3. T4 to T8 and T6 to T9 crests are present. Z is quite small.

On M₁ there is no trace of either Sm or Z. The principal cusps are slightly alternate with S1 larger than Sv and set somewhat forward of it. Posterointernal crests from S1 and Sv join in the midline of the tooth halfway below the cusp apex and, somewhat lower, these are in turn joined by anterointernally directed crests from Epd and Eod. End and Td also join about halfway down their medial slopes. There is no eocrista. There are labial angular cusps at the base of Eod and Td.

Discussion.—Both of these species display a mosaic of what are considered by Missone (1969) to be primitive characters. The posterior position of T1 and T4, the relatively short M¹ in relation to M², the lack of M¹–M² overlap, and the small number of cingular cusps on M₁ are probably primitive traits. In contrast, the small T9, small upper Z



Figs. 11, 12.—*Anthracomys* sp. A. 11) T-3808, right M^2 . 12) T-4212, right M_2 .

Figs. 13–16.—*Anthracomys* sp. B. 13) T-4211, left M^1 . 14) T-4242, left M^3 . 15) T-4241, right M_1 . 16) T-4210, right M_1 .

and absence of Sm and Z on M_1 are considered to be advanced characters. The lower Z is present in both *Progonomys* and *Parapodemus* but absent in *Anthracomys*. There is no stephanodonty in the former two genera, whereas there is some indication of this condition in *Anthracomys*. The upper Z is small in all three genera.

Anthracomys quite probably evolved from *Progonomys*, involving loss of Sm, reduction of upper Z, loss of lower Z, and a trend towards stephanodonty with T3-T6, T6-T9, and T4-T8 crests. Primitive characters of *Progonomys* retained in *Anthracomys* include the cingulum with only two small cusps on M_1 , the posterior position of T1 and T4, and the still relatively short M_1^1 .

Anthracomys sp. A is somewhat smaller than *A. miocaenicus* from Morocco, but this may not be significant considering that only two teeth are known from Tunisia. The larger species, *Anthracomys* sp. B, is perhaps about the same size as *A. filifilae*. There is too little material of both species to make any definitive specific assignments.

SUMMARY OF KECHABTA FORMATION LOCALITIES AND FAUNAS

Oued Mellegue, near base of unit

Family Equidae

Hipparion sp. (Biely et al., 1974)

Oued Mellegue (Voie Ferrée), near top of unit

Family Soricidae

Soricid indet.

Family Sciuridae

Atlantoxerus sp.

Family Muridae

Anthracomys sp. A.

Anthracomys sp. B.

Family Ochotonidae

Prolagus sp.

Araguib Kammra C

Family Cricetidae

Myocricetodon sp. cf. *M. seboui*

Araguib Kammra B

Family Sciuridae

Atlantoxerus sp.

MDM Locality, Sidi Ounis, near Zag et Tir

Family Erinaceidae

Schizogalerix ?moedlingensis

Family Cricetidae

Zramys jaegeri, new species

Family Sciuridae
Atlantoxerus sp.

Except for *Atlantoxerus* sp., there are no species common to any of the localities, making correlations difficult. On physical stratigraphic criteria, the Araguib Kammra and MDM localities should be the youngest, as the former is near the contact with the Oued bel Khedim Formation and the latter is below the freshwater limestones that are presumed to be correlative with the Oued bel Khedim (Burolet, 1956). The Voie Ferrée locality occurs below an angular unconformity, and at that locality the Oued bel Khedim, if it was ever present, is presumed to have been lost by erosion.

The only biostratigraphically useful species from the Araguib Kammra is *Myocricetodon* sp. cf. *M. seboui* which could range from mid-Vallesian to mid-Turolian (Jaeger, 1977b). Although *Zramys jaegeri* has not been reported from elsewhere, the stage of evolution of the species compared to that of other species of *Zramys*, indicates that it may be Turolian, possibly as young as mid-Turolian. The *Anthracomys* from Voie Ferrée is comparable with the *Anthracomys* from Amama 2 and Khendek el Ouach (Jaeger, 1977b) and therefore may also be mid-Turolian, as is the species of *Schizogalerix*.

Jaeger (1977b) reported that his locality at Djebel Semmene was probably mid-Vallesian, a conclusion which seems highly probable. As the lower part of the Kechabta Formation may well intertongue with the upper part of the Hakima Formation (Biely et al., 1974), the range of mid-Vallesian to mid-Turolian for the entire Kechabta Formation is reasonable.

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THE ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA. III. REPRODUCTIVE BIOLOGY AND POPULATION ECOLOGY

KARL E. STREILEIN¹

ABSTRACT

The timing of reproduction is critical in an environmentally unpredictable area such as the Caatinga region of Brazil. Most of the small mammal species in the Caatinga reproduce year round but with varying degrees of success. The caviomorph rodents and marsupials are able to maintain higher population levels than the murid rodents, with a generally lower gross output of young.

INTRODUCTION

Lowland tropical areas generally do not experience the temperature and photoperiod extremes typical of the higher latitudes. In a completely aseasonal tropical area then, one might expect to observe reproductive patterns and strategies in the small mammal fauna which differ significantly from those seen in ecologically similar or taxonomically related species in the higher latitudes. Most tropical areas do, however, experience seasonality with respect to the annual rainfall regime.

Knowledge of patterns of reproduction is lacking for most species of tropical small mammals, but the available data reveal the existence of several reproductive strategies. Fleming (1973) summarized the available information on Panamanian small mammals that experience wet-dry seasonality and found that the three marsupial species were seasonally polyestrous while the rodents included year-round polyes-

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trous species, seasonally polyestrous species, and seasonally monestrous species. Adequate data existed for only 15 of an estimated 51 rodent species, so it is uncertain which pattern is most common. O'Connell (1979) has suggested that several Venezuelan marsupials are seasonally polyestrous. Seasonal breeding has also been observed in rodent species in other tropical areas. Two species of heteromyid rodents inhabiting seasonal tropical forests in Costa Rica exhibited varying degrees of seasonality in reproduction (Fleming, 1974). Murid rodents in equatorial Africa were also shown to have distinct breeding periods related to seasonality of rainfall (Delany and Neal, 1969; Field, 1975).

Most of the studies on the population ecology of small mammals have also been conducted in relatively mesic areas that experience predictable seasonality (Fleming, 1971, 1972, 1974; Heaney and Thorington, 1978; Smythe, 1978; O'Connell, 1979). The demographic characteristics of the populations generally reflected seasonal changes, with fluctuations in density and shifts in survivorship and age structure.

The Caatinga of Brazil, however, is semiarid and subject to an unpredictable rainfall regime. One objective of this study, then, was to determine the general types of reproductive strategies that have evolved in response to the fluctuating, semiarid Caatinga environment and to assess the possible adaptive value of each strategy. The second objective was to obtain baseline population data on the small mammals and to examine the adaptive significance of particular parameters or trends.

MATERIALS AND METHODS

Reproduction

Reproductive data were gathered from animals captured and released on the grid, from animals collected at other sites within the Municipality of Exu, and from individuals maintained in the laboratory. Animals live-trapped on the grid were examined at each capture for external reproductive characters, including position of testes in males and condition of vagina (perforated or not), presence of palpable embryos or attached young, and lactation state (non-lactating, lactating, or post-lactating) for females. External reproductive characters were also recorded for kill-trapped specimens as well as supplemental data on size of testes and general condition of the epididymis in males and the relative degree of uterine vascularization, and number, location, and general state of development of embryos in females.

Data from live-trapped individuals on the grid and kill-trapped animals from other sites were combined (Tables 1-2). The number of pregnant females is underestimated because palpable embryos were detectable only in advanced states. Corresponding months in different years were combined after statistical tests for possible differences proved to be insignificant.

Population Ecology

A permanent 12 by 12 live trapping grid with 15 m spacing between traps (2.7 ha) was established in January, 1977 at Fazenda Batente, six km southeast of Exu, Pernambuco (7°31'S, 39°43'W) after preliminary trapping during December 1976 established the suitability of the site. Three distinct microhabitats were included—rocky areas (lajeiros), thorn scrub (Caatinga Baixa), and old field. Trapping was conducted from January 1977 through February 1978. One large, collapsible Sherman live trap and a larger, wire live trap manufactured in Brazil were set at alternate stations. Traps were rotated after three to 14 days, depending upon total number of days trapped each month, weather conditions, and trap success. Because capture success was extremely low during the first months, the trapping period was slowly increased through July; thereafter, traps were set every possible day for the duration of the study. Trapping effort per month by microhabitat type is summarized in Table 3. Traps were opened just before dusk and checked the following morning to avoid the high daily temperatures. A variety of baits (Brazil nuts, peanuts, field corn, pineapple, and other fruits) were used because the availability of each item varied a great deal.

Each individual was toe-clipped when first captured. Information recorded at each capture included identification number, species, sex, location on grid, weight, and external reproductive condition. Weights were obtained with 500 g or 1500 g Pesola balances.

Capture records were then used to estimate monthly population sizes by direct enumeration (Fleming, 1971). In this method, each monthly estimate is comprised of three general classes of animals, including animals captured for the first time, previously marked individuals recaptured that month, and individuals not captured in that particular month but which were captured in both previous and subsequent months. The main advantage of direct enumeration is the elimination of bias introduced into monthly estimates by nonrandom sampling (for example, trapping) of the population. This method does, however, assume that animals which disappear from the capture records for one or more months and subsequently reappear actually remained on the grid but failed to enter traps.

Capture records were also used to determine home range size for every animal with four or more captures. Individual home range size was calculated by the minimum area technique (Stickel, 1954).

RESULTS

Reproduction

Monodelphis domestica.—This small marsupial apparently breeds throughout the year as evidenced by the presence of lactating females in eight of the ten months in which adult females were examined (Table 1) and the dates of appearance of immature animals on the grid and at supplemental collecting sites. The maximum number of litters produced by a female on the grid was two, but this low number is largely a function of brief residency on the grid (maximum residency was only six months). The shortest period between recorded pregnancies was seven to eight weeks. Lactation generally ceased after six to eight weeks in females trapped on the grid or maintained in the laboratory. A female could thus produce five or six litters in one year under optimal conditions. Most of the females examined were young adults

Table 1.—*Reproductive condition of adult female marsupials and rodents.*

Month	Number of individuals			Total reproductively active	Total not active	Total
	Pregnant	Lactating or postlactating	Nonlactating			

<i>Monodelphis domestica</i>						
July	—	—	—	—	—	—
August	0	0	1	0	1	1
September	0	1	2	1	2	3
October	0	2	2	2	2	4
November	0	2	1	2	1	3
December	0	2	4	2	4	6
January	0	2	3	2	3	5
February	0	4	2	4	2	6
March	0	1	2	1	2	3
April	0	2	2	2	1	3
May	—	—	—	—	—	—
June	0	0	1	0	1	1
<i>Didelphis albiventris</i>						
July	0	0	2	0	2	2
August	0	0	5	0	5	5
September	0	0	4	0	4	4
October	0	0	2	0	2	2
November	0	8	1	8	0	8
December	0	1	1	1	0	1
January	0	3	0	3	0	3
February	0	8	0	8	0	8
March	0	1	0	1	0	1
April	—	—	—	—	—	—
May	0	0	1	0	1	1
June	0	0	1	0	1	1
<i>Bolomys lasiurus</i>						
July	—	—	—	—	—	—
August	—	—	—	—	—	—
September	0	0	3	0	3	3
October	0	0	3	0	3	3
November	0	1	5	1	5	6
December	0	0	1	0	1	1
January	1	1	8	2	8	10
February	0	1	0	1	0	1
March	0	1	0	1	0	1
April	3	0	5	3	2	5
May	—	—	—	—	—	—
June	—	—	—	—	—	—
<i>Calomys callosus</i>						
July	—	—	—	—	—	—
August	—	—	—	—	—	—
September	0	1	0	1	0	1
October	0	0	2	0	2	0
November	1	1	1	2	0	2

Table 1.—Continued.

Month	Number of individuals			Total reproductively active	Total not active	Total
	Pregnant	Lactating or postlactating	Nonlactating			
December	—	—	—	—	—	—
January	—	—	—	—	—	—
February	0	2	0	2	0	2
March	—	—	—	—	—	—
April	0	1	0	1	0	1
May	0	0	1	0	1	1
June	—	—	—	—	—	—
<i>Wiedomys pyrrhorhinos</i>						
July	—	—	—	—	—	—
August	1	2	0	3	0	3
September	0	3	0	3	0	3
October	0	1	0	1	0	1
November	—	—	—	—	—	—
December	0	1	0	1	0	1
January	—	—	—	—	—	—
February	—	—	—	—	—	—
March	0	0	1	0	0	1
April	—	—	—	—	—	—
May	0	1	0	1	0	1
June	—	—	—	—	—	—
<i>Galea spixii</i>						
July	1	1	0	1	0	1
August	3	8	2	8	2	10
September	15	15	5	17	3	20
October	2	3	0	3	0	3
November	5	4	1	5	0	5
December	4	8	7	9	6	15
January	2	3	7	3	7	10
February	2	4	2	4	2	6
March	1	1	1	1	0	1
April	0	1	0	1	0	1
May	—	—	—	—	—	—
June	3	4	0	4	0	4
<i>Thrichomys apereoides</i>						
July	1	1	6	2	5	7
August	2	2	7	3	4	7
September	9	3	11	10	4	14
October	3	6	6	8	4	12
November	1	8	8	10	5	15
December	1	0	14	1	14	13
January	2	0	12	2	10	12
February	5	1	12	6	7	13
March	2	2	2	4	0	4
April	1	7	1	8	0	8
May	—	—	—	—	—	—
June	—	—	—	—	—	—

Table 2.—Litter size in 10 species of small mammals in the Caatinga, Brazil.

Species	Number of litters	Mean	Standard Deviation	Range	Authority
Marsupialia					
Didelphidae					
<i>Monodelphis domestica</i>	7	8.4	2.6	6–11	Present study
<i>Didelphis albiventris</i> ¹	12	6.2	2.2	3–9	Present study
Rodentia					
Muridae					
<i>Oryzomys eliurus</i> ^{2,3}	18	3.0	1.3	1–5	Mello (1978a)
<i>Oryzomys subflavus</i>	2	5.5	—	—	Present study
<i>Bolomys lasiurus</i>	7	3.3	0.5	3–4	Present study
<i>Bolomys lasiurus</i>	—	6.0	—	1–13	Karimi et al. (1976)
<i>Calomys callosus</i>	5	4.4	2.3	2–8	Present study
<i>Calomys callosus</i> ^{2,3}	27	4.5	1.8	2–9	Mello (1978b)
<i>Wiedomys pyrrhorhinos</i>	5	3.8	1.8	1–6	Present study
Caviidae					
<i>Kerodon rupestris</i> ²	17	1.4	0.5	1–2	Lacher (1980)
<i>Galea spixii</i>	24	3.0	1.0	1–5	Present study
<i>Galea spixii</i> ²	10	2.2	0.9	1–4	Lacher (1980)
Echimyidae					
<i>Thrichomys apereoides</i>	21	3.1	1.2	1–6	Present study

¹ Includes three litters from lactating females collected on the Chapada do Araripe.

² Data based solely on laboratory specimens.

³ Parental stock captured in Cerrado biome in Goiás, Brazil.

with body weights between 50 to 60 grams; no females weighing less than 50 grams exhibited reproductive activity. Approximately five to seven months were required to attain sexual maturity. Observed litter size ranged from 6 to 11 with a mean of 8.4 (Table 2).

Didelphis albiventris.—This species exhibits synchronous breeding with births occurring in November and December. Lactating females were captured only between November and March (Table 1). Every female examined during this period was reproductively active, indicating a concentrated reproductive effort by this species. Females produced only one litter per breeding season; however, one individual which lost its entire litter (born in November) was able to produce a second litter (in January). Young born in November and December initially appear in traps as subadults in late April or May and are sexually mature by November. Litter size ranged from 3 to 9 with a mean of 6.2 (Table 2).

Bolomys lasiurus.—Data from this study were too fragmentary to conclusively establish the reproductive pattern. However, Karimi et

al. (1976) autopsied several thousand females captured in the Municipality of Exu and found that most of the pregnant females recorded were collected during the months of April, May and June, indicating a seasonal peak in breeding. A low level of reproductive activity may begin as early as November (Table 1). Females apparently produced more than one litter per year and the young matured rapidly. In this study, mean litter size was 3.3 with a range of 3 to 4 (Table 2), but based on a much larger number of autopsied females, Karimi et al. (1976) reported a mean of six young per litter and a range of 1 to 13.

Calomys callosus.—Only eight females were captured, six of which were reproductively active, including two in February, one in April, one in September, and two in November (Table 1). Litter size ranged from 2 to 8 with a mean of 4.4 (Table 2). *Calomys callosus* bred under laboratory conditions averaged 4.5 young per litter with a range of 2 to 9. (Mello, 1977, 1978b).

Wiedomys pyrrhorhinos.—All but one of the adult females examined were reproductively active (Table 1). Litter size ranged from 1 to 6, with a mean litter size of 3.8 (Table 2). Captures were concentrated at the end of the dry period (August, September, and October). The single specimen in December was taken from a nest with one subadult; size of the subadult indicated that parturition occurred in early November or late October. This period of reproductive activity transpires as the seeds of many legumes and other plants are maturing (August through November).

Kerodon rupestris.—Lacher (1979) reported a mean litter size of 1.4 with a maximum of two young per litter; captive females reproduced throughout the year. Six litters per year may be possible under optimal conditions.

Galea spixii.—The majority of the females examined were reproductively active regardless of time of the year (Table 1). Some females on the grid were continuously reproductively active during their entire residency. Gestation period was approximately 7 to 8 weeks and females underwent a postpartum estrous; six or seven litters per year are possible under the correct conditions. Mean litter size was 3.0 with a range of 1 to 5 (Table 2).

Thrichomys apereoides.—Some reproductive activity existed in every month of the year (Table 1). Very few females were active in December and January; this is just after the peak of seed maturation and prior to the initiation of fruit maturation. At this time, many of the females were relatively young adults born between February and April and as such, had just completed the seven to nine months required to attain sexual maturity. Adults on the grid produced two to three litters per year with a four to six month interval between births. Litter size averaged 3.1 with a range of 1 to 6 (Table 2).

Table 3.—*Trapping effort on the grid from January 1977 through February 1978. Percentage of total in parentheses.*¹

Month	Number of days trapped	Number of trap nights			
		Rock	Thorn scrub	Old field	Total
1977					
January	3	186	192	54	432
February	6	384	368	112	864
March	7	452	424	132	1008
April	6	390	360	114	864
May	7	434	448	42	924
June	9	382	526	62	970
July	13	836	766	88	1590
August	31	2000	1818	212	4030
September	25	1872	1382	120	3374
October	20	1320	1224	124	2668
November	15	975	930	90	1995
December	12	852	648	96	1596
1978					
January	20	1420	1080	160	2660
February	12	780	744	72	1596
Total	186	12,483	10,910	1478	24,871
		(.498) ¹	(.436)	(.066)	

Population Ecology

The monthly profiles of population size and composition of the four species with adequate sample sizes are presented in Table 5.

Subadult *D. albiventris* appeared in only two months, April and May. This trend reflects the restricted breeding season (November–December) and rapid rate of growth in the young. The increased number of individuals on the grid in the dry months (June through October) was a result of both internal and external recruitment. *Monodelphis domestica* density also increased during dry months. This trend was largely a result of subadults reaching adult size. The low number of *G. spixii* subadults is significant because most of the adult females examined on the grid and elsewhere in the Municipality of Exu were large, reproductively active individuals. High levels of reproductive activity and an adult population comprised mainly of larger, older individuals imply that the mortality rate of young animals is very high relative to that of the adults. Subadult *T. apereoides* comprised a much larger portion of the population than did their *Galea* counterparts, and at times exceeded the number of adults. Adult females were generally twice as numerous as adult males throughout the course of the study.

Table 4.—Maximum estimated reproductive capability of marsupials and caviomorph rodents occurring on the grid.

Species	Reproductive pattern	Mean litter size	Estimated maximum number litters per year	Maximum reproductive effort per year
Marsupialia				
Didelphidae				
<i>Monodelphis domestica</i>	Year-round polyestrous	8.4	5–6	42–50
<i>Didelphis albiventris</i>	Restricted monestrous	6.2	1	6
Rodentia				
Caviidae				
<i>Kerodon rupestris</i>	Year-round polyestrous	1.4	5–6	7–8
<i>Galea spixii</i>	Year-round polyestrous	3.0	6–7	18–21
Echimyidae				
<i>Thrichomys apereoides</i>	Year-round polyestrous	3.1	2–3	6–9

The population density of *T. apereoides* was unexpectedly high; this species was restricted to rocky areas (Streilein, 1981*b*) which comprised only 50% of the grid.

Home range sizes for these species are recorded in Table 6. Individual variation within each species was very high with the standard deviation exceeding the group mean in a number of instances.

The number of individuals in each species trapped on the grid is presented in Table 7. Two of the species are underrepresented even though the cumulative number of trap nights on the grid was very large ($\approx 25,000$). *Kerodon rupestris* was actually rather common but was not easily enticed into entering traps; diurnal observations sometimes revealed more individuals in one small portion of the grid than were captured in 14 months of trapping. The use of runways by *G. spixii* was the primary factor in the underrepresentation of this species. Mean number of captures per individual (Table 7) and percentage of individuals never recaptured (Table 8) are two other components of relative trappability. *Monodelphis domestica* and *D. albiventris* females and both sexes of *T. apereoides* exhibited the least degree of trap avoidance after their initial capture (13–21%), whereas a greater portion (44–57%) of both sexes of *G. spixii* and *D. albiventris* males was captured only once. The duration of individual residency on the grid was extremely variable in every species as evidenced by the very large standard deviations from the mean in every group (Table 9). The mean lengths of residency ± 1 SD overlapped to a large extent both within and among species.

Table 5.—Direct enumeration estimates of population size for common species on the grid by month and year.

Species	1976						1977						1978					
	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F			
Marsupialia																		
Didelphidae																		
<i>Monodelphis domestica</i>																		
Adult	5	1	3	2	1	0	1	0	2	7	9	5	6	11	8			
Subadult	0	0	0	0	1	0	0	2	4	3	2	0	1	0	2			
Total	5	1	3	2	2	0	1	2	6	10	11	5	7	11	10			
<i>Didelphis albiventris</i>																		
Adult	1	1	3	2	0	4	7	7	13	11	8	6	4	5	3			
Subadult	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0			
Total	1	1	3	2	2	6	7	7	13	11	8	6	4	5	3			
Rodentia																		
Caviidae																		
<i>Galea spixii</i>																		
Adult	14	9	10	7	4	3	6	4	7	10	7	9	9	6	2			
Subadult	1	0	0	0	1	2	0	2	0	0	0	0	1	1	0			
Total	15	9	10	7	5	5	6	6	7	10	7	9	10	7	2			
Echimyidae																		
<i>Thrichomys apereoides</i>																		
Adult																		
Male	0	1	1	1	0	0	0	1	4	5	5	9	5	6	4			
Female	2	2	3	2	2	3	3	6	8	10	11	11	12	10	9			
Subadult																		
Male	0	0	0	0	0	2	0	1	3	10	9	4	4	3	2			
Female	1	1	1	1	1	3	3	2	5	9	6	7	2	2	1			
Total	3	4	5	4	3	8	6	10	20	34	31	31	23	21	16			

Table 6.—Size of home range for common species on the grid (m^2).

Species	Number of individuals	Mean home range size ± 1 SD
Marsupialia		
Didelphidae		
<i>Monodelphis domestica</i>	11	1472.7 \pm 859.3
Adult $\delta \delta$	6	1209.4 \pm 1050.4
Adult $\eta \eta$	5	1788.8 \pm 487.8
<i>Didelphis albiventris</i>	16	7022.9 \pm 5047.8
Adult $\delta \delta$	10	7705.3 \pm 5306.3
Adult $\eta \eta$	6	5885.4 \pm 4575.3
Rodentia		
Caviidae		
<i>Galea spixii</i>	14	1181.3 \pm 1322.7
Adult $\delta \delta$	6	1462.5 \pm 1999.5
Adult $\eta \eta$	8	970.3 \pm 524.0
Echimyidae		
<i>Thrichomys apereoides</i>	38	1906.3 \pm 1932.4
Males	17	1987.8 \pm 1554.1
Females	21	1840.2 \pm 2228.4
Adults	22	2022.4 \pm 1517.3
Subadults	16	1746.5 \pm 2437.4

DISCUSSION

Reproduction requires a considerable investment of time and energy, and may also entail other costs, such as increased exposure to predators; successful strategies must therefore minimize the effort expended in reproduction at inappropriate times. Exogenous factors, such as photoperiod, mean temperature, and initiation or cessation of wet phases are typically correlated with intervals of favorable environmental conditions suitable for reproduction. In an environmentally unpredictable area, however, these exogenous factors may not be reliable indicators of either the onset or duration of favorable conditions. Two general strategies which should minimize wasted effort in unpredictable areas are: 1) consistently concentrate reproductive effort in the interval when favorable conditions have the highest probability of occurring; or 2) retain reproductive flexibility, breeding whenever and as long as environmental conditions are appropriate. The ability to accurately track environmental conditions is a requirement for both strategies. Species with *r*-selected traits, such as short gestation, large litter size, and early maturation (see Stearns, 1976, 1977, and Horn, 1978, for further discussion of life history traits) might be expected to

Table 7.—*Number of individuals captured on the grid. Mean number of captures per individual in parentheses.*

Species	Number of individuals		
	Males	Females	Total
Marsupialia			
Didelphidae			
<i>Monodelphis domestica</i>	23 (2.7)	15 (6.1)	38 (4.0)
<i>Didelphis albiventris</i>	22 (8.0)	10 (7.8)	32 (8.0)
Rodentia			
Muridae			
<i>Bolomys lasiurus</i>	3 (3.0)	3 (1.7)	6 (2.3)
<i>Calomys callosus</i>	4 (3.5)	2 (1.5)	6 (2.8)
<i>Wiedomys pyrrhorhinos</i>	2 (1.0)	1 —	3 (1.0)
Caviidae			
<i>Kerodon rupestris</i>	2 (1.0)	3 (1.0)	5 (1.0)
<i>Galea spixii</i>	23 (3.4)	35 (2.9)	58 (3.1)
Echimyidae			
<i>Thrichomys apereoides</i>	29 (11.7)	30 (16.0)	59 (13.9)

exhibit the second strategy because these species are ideally suited to respond to ephemeral favorable conditions with a rapid, intense reproductive effort.

Continuous reproduction may also be a viable strategy for small mammal species faced with an unpredictable environment, but the accompanying costs are high. Individuals would reproduce when it is energetically feasible, even at inappropriate times, for example, those intervals in which the probability of young surviving to reproduce is so small that the benefit obtained is far less than the individual advantage gained by hoarding energy and deferring reproduction until the advent of favorable conditions. If the individuals are capable of monitoring environmental fluctuations, even relatively short-lived species should benefit by delaying reproduction when adverse conditions prevail, if by doing so, they substantially increase their probability of surviving to successfully reproduce in the near future. A species with a haphazard reproductive pattern will only be able to persist in an area through fortuitous co-occurrences of reproductive effort and favorable conditions.

The Caatinga is characterized by a high degree of environmental uncertainty. The rainfall regime is extremely erratic with respect to both timing and amount of precipitation. In the area around Exu, for example, rainfall sufficient to produce a relative water surplus may

Table 8.—Percent of individuals captured only once on the grid.

Species	Number of individuals captured	Number of individuals captured only once	Percentage
Marsupialia			
Didelphidae			
<i>Monodelphis domestica</i>	38	11	28.9
♂ ♂	23	8	34.8
♀ ♀	15	3	21.4
<i>Didelphis albiventris</i>	32	12	37.5
♂ ♂	22	10	47.6
♀ ♀	10	2	20.0
Rodentia			
Caviidae			
<i>Galea spixii</i>	58	30	51.7
♂ ♂	23	10	43.5
♀ ♀	35	20	57.1
Echimyidae			
<i>Thrichomys apereoides</i>	59	10	17.0
♂ ♂	29	6	20.7
♀ ♀	30	4	13.3

occur in any month between October and May but there is no consistent "rainy season." Rainfall in any particular month cannot be correlated with rainfall in previous or subsequent months. The probability of a month receiving sufficient rainfall in the October–May interval ranged from 7.1 to 78.6% between 1964–1978 (Streilein, 1982a). In effect, over a span of years, the small mammals are subject to every possible combination of wet and dry months, including extended droughts. The low level of water retention in the Caatinga system compounds the problem. There is a unique mitigating factor, however. The Caatinga contains a large number of granitic formations that function as relatively stable microrefugia from the wildly fluctuating ambient conditions.

Didelphis albiventris was the only Caatinga species which exhibited synchronous, monestrous reproduction; parturition occurred in November or early December and included all adult females. November and December are the first months in which rainfall surpluses sometimes occurred after the consistently dry months (Streilein, 1982a), but perhaps a more important factor in the success of this mode of reproduction is the high probability of sufficient rainfall in March and April

Table 9.—Length of residency (in days) of common species on the grid.

Species	Number of individuals	Mean \pm 1 SD
Marsupialia		
Didelphidae		
<i>Monodelphis domestica</i>	38	55.9 \pm 58.6
♂ ♂	23	42.7 \pm 47.1
♀ ♀	15	72.5 \pm 69.0
Adults	25	64.7 \pm 65.9
Subadults	13	38.3 \pm 37.6
<i>Didelphis albiventris</i>	32	75.3 \pm 66.3
♂ ♂	22	80.2 \pm 70.6
♀ ♀	10	68.6 \pm 63.9
Adults	29	69.5 \pm 65.9
Subadults	3	124.5 \pm 64.3
Rodentia		
Caviidae		
<i>Galea spixii</i>	58	77.9 \pm 96.6
♂ ♂	23	69.9 \pm 86.8
♀ ♀	35	84.8 \pm 106.9
Adults	51	81.7 \pm 99.2
Subadults	7	28.5 \pm 20.5
Echimyidae		
<i>Thrichomys apereoides</i>	58	110.3 \pm 103.0
♂ ♂	29	63.3 \pm 52.6
♀ ♀	29	151.8 \pm 118.8
Adults	35	147.7 \pm 105.0
Subadults	23	33.2 \pm 31.4

when the young are weaned. An element of risk is inherent in this strategy, as the reproductive effort for an entire year might be lost if severe conditions strike during or immediately after the weaning period. This type of reproductive strategy is probably feasible only for those species in which adults have a high enough probability of surviving more than one year.

Data on the murid rodents were not conclusive with regard to timing and extent of reproduction because very low population levels prevailed throughout the course of the study. The limited data do indicate that *Wiedomys pyrrhorhinos* and *Calomys callosus* breed at a high rate throughout the year, even during periods of intense, prolonged water stress, but very few of the young enter the population as adults. This suggests but does not demonstrate conclusively a "hit or miss" approach in which many young are produced at whatever time in the hope that future conditions will permit some to survive.

Karimi et al. (1976) reported a reproductive peak in *Bolomys lasiurus* during the months of April, May, and June in their study. This peak occurred immediately after an extended interval of water surplus. *Bolomys lasiurus* may have developed a very conservative reproductive strategy, with a major reproductive effort commencing only after favorable conditions have been established beyond doubt, thus totally avoiding wasted effort. Conversely, *B. lasiurus* may be poorly attuned to the climatic vagaries of the Caatinga and thus be incapable of a rapid response to the onset of the ephemeral, favorable conditions. The limited reproductive data collected in this study and consideration of the distribution pattern (Streilein, 1982b) of *B. lasiurus* suggest that the second alternative is correct. All of the murids are polyestrous species with reasonably large reproductive capabilities but none clearly exhibit reproductive patterns which parallel the two basic strategies that should theoretically be most successful in an unpredictable environment.

The remaining species, *Monodelphis domestica*, *Galea spixii*, *Thrichomys apereoides*, and *Kerodon rupestris*, reproduce throughout the year (Table 4). Continual reproduction does not appear to correspond with either of the general reproductive strategies one expected in an environmentally unpredictable area. Examination of another aspect of the ecology of these species resolves this apparent contradiction. *Kerodon rupestris*, *T. apereoides*, and *M. domestica* are microhabitat specialists (Streilein, 1982b) which preferentially utilize the relatively mesic granitic outcroppings, and as such are buffered during periods of severe water stress. Microhabitat specificity in these species thus functions in the maintenance of relatively favorable conditions with respect to water stress by moderating the effects of environmental unpredictability; none of the murid rodents have developed an affinity for these advantageous habitats (Streilein, 1982b). Year round reproduction in this instance is compatible with the second strategy, in which reproduction should occur whenever environmental conditions permit. *Galea spixii* also breeds throughout the year (Table 1), including periods of severe water stress which should not be amenable to successful reproduction. This species utilizes the rock outcroppings to a lesser extent. The high rate of reproduction is apparently needed to compensate for the low rate at which young enter the adult population. A continuously high rate of reproduction may be a feasible strategy in an unpredictable environment but the accompanying costs are high, in terms of wasted energy and increased risks. This type of reproductive strategy in the Caatinga, where relatively stable habitats are readily available, may be interpreted as a low degree of adaptation to the prevailing conditions.

Every species invading a new habitat requires a period of time to

adapt to the new set of environmental conditions, unless it is adequately preadapted, and an unpredictable environment will present additional problems, thus presumably increasing the period of time required to achieve a high degree of adaptation. The relative degree of adaptation may be inferred by examining certain critical aspects of the biology of the inhabitants. In the Caatinga, reproductive strategies and microhabitat utilization patterns should be particularly informative. Without an appropriate response to the new set of conditions, the species will not be successful. If these premises are accepted, the relative degree of adaptation should generally reflect the amount of time a species has existed in the area.

The biogeographic history of South America as outlined by Patterson and Pascual (1972) has the ancestral stock of marsupials arriving in the Cretaceous, with didelphids occurring by the late Paleocene, caviomorph rodents appearing by the early Oligocene, and murid rodents arriving at the Pliocene-Pleistocene interface. Marsupials and caviomorph rodents have thus had a much longer period of time during which natural selection processes would be operating to produce suitable adaptations for particular environments than the more recently arrived murids. Hershkovitz (1966, 1972) has proposed, however, that murids began arriving much earlier, perhaps in the Miocene; if this is the case, murids have also had a long period of time for adaptation. Marshall (1979) also supports the earlier arrival date but postulates that large scale dispersal did not occur until the first glaciation in South America.

In the Monte Desert of Argentina, the marsupials and caviomorphs are more desert-adapted in general than the murids (Mares, 1973, 1980). Examination of the reproductive patterns, in conjunction with water conservation capabilities and distribution patterns, in the Caatinga small mammal fauna produces a similar conclusion; the marsupials and caviomorphs generally exhibit a greater degree of specialization for the particular set of environmental conditions in the Caatinga than the murids. This relationship holds true even though the extenuating circumstances are different; Mares (1980) has suggested that some murids that reached the Monte were apparently preadapted for xeric conditions as they moved south along the Andes. In contrast, the Caatinga is far removed from the Andean dispersal route, thus decreasing the likelihood of suitable preadaptation.

The population levels of the murid rodents were very low throughout the course of this study. Examination of AGGEU's (a public health agency responsible for monitoring the small mammal species that harbor bubonic plague vectors) trapping records for the Municipality of Exu revealed that low population levels are typical for *Oryzomys elingurus*, *O. subflavus*, *Calomys callosus*, and *Wiedomys pyrrhorhinos*.

Bolomys lasiurus, on the other hand, varies from rare to abundant. During one three-month period in 1977, the professional collectors of AGGEU trapped one *B. lasiurus* in 29,250 trap nights—a capture success of 0.00003%. Conversely, a mark-release experiment conducted several years earlier by Karimi et al. (1976) produced an estimated population density of 187/ha. Emigrants from temporally dense populations form the nucleus for additional eruptions. Successful emigration is necessary for *B. lasiurus* to persist in the Caatinga because the only habitats occupied are ephemeral in nature. Before the arrival of slash and burn agriculture, this species probably depended on sporadic natural events (lightning fires, for example) for the creation of suitable habitats.

Low population levels, however, are not characteristic of the murid species in the adjoining Cerrado region. Mello (1977) reported that *O. eliurus*, *B. lasiurus*, and *C. callosus* are the three most abundant rodents, with *O. eliurus* exhibiting two population peaks per year. Similar habitats are occupied by the same species in the Cerrado and Caatinga and mean yearly rainfall is not substantially different, but population levels differ drastically. The fundamental difference between the two regions is in the predictability of rainfall. Animals in the Caatinga cannot reproduce with the certainty that environmental conditions will remain favorable whereas highly predictable seasonality permits continuity in the Cerrado.

The caviomorphs maintain higher population levels than the murids. *Kerodon rupestris* and *Thrichomys apereoides* preferentially utilize the more stable habitats, granitic outcroppings, and are thus able to successfully reproduce throughout the year. *Galea spixii* also uses the outcroppings to a certain extent. Continuous successful reproduction provides a constant influx of individuals into the populations. Another contributing factor, perhaps, is that the precocial young of the caviomorphs are better able to withstand environmental fluctuations than the altricial murids.

The two marsupial species maintained intermediate population levels, but with very different tactics. *Didelphis albiventris* had a single, restricted period of intense reproductive activity, with the emergence of subadults coinciding with the period having the highest probability of sufficient rainfall. *Monodelphis domestica*, on the other hand, preferentially utilizes the granitic outcroppings and breeds throughout the year. *Monodelphis domestica* has a much higher reproductive potential (Table 4), but their much smaller body makes them vulnerable to a wider variety of predators and the young are not protected by a marsupium. Some mortality was observed in *D. albiventris* pouch litters; the loss of recent young in *M. domestica* is probably much greater.

Mean home range sizes of the common species on the grid were relatively small, less than 0.2 ha in most cases (Table 6). Small home range sizes in the habitat specialists, *T. apereoides* and *M. domestica*, were probably a function of the structural complexity in the rock outcroppings. The grid was also too small to encompass the occasional long movements undertaken by *D. albiventris* and *G. spixii*, producing the moderate length of residency and large portion of individuals captured only once. The short, mean length of residency on the grid for *M. domestica* probably reflects a high mortality rate. Most *T. apereoides* adults were originally trapped on the grid as subadults, producing a reasonably long mean length of residence for this species.

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THE SRI LANKAN GENUS *ASPIDURA* (SERPENTES,
REPTILIA, COLUBRIDAE)

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ABSTRACT

Review of a collection of snakes of the genus *Aspidura* recently made on Sri Lanka, and of some museum material, including all available types, documents the occurrence of the six species—*A. brachyorrhos*, *copei*, *deraniyagalae* new species, *drummondhayi*, *guentheri*, and *trachyprocta*. The forms are defined and illustrated, their geographical and altitudinal ranges clarified, and available ecological data reviewed. The review suggests that the genus is restricted to Sri Lanka and that the record from Malé Atoll in the Maldivé Archipelago represents an error.

INTRODUCTION

The surveys of the amphibians and reptiles of India culminating in the monumental three volume report of Malcolm Smith (1931, 1935, 1943) have left us with characterizations of some major categories of the herpetofauna of that subcontinent. Unfortunately, they also incorporate the seeds of confusion. Many of the specimens upon which they are based were inadequately characterized, and elevational and ecological information were generally missing. Locality names were sometimes misinterpreted, and the samples were inadequate to describe the several kinds of variability.

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As a by-product of an attempt better to understand the biology of uropeltid snakes, a well-documented series of the small and crepuscular reptiles and amphibians of Sri Lanka is being assembled. We here review the small snakes of the genus *Aspidura* in order more accurately to characterize the definitions and distributions of the various species. This report reviews material recently collected and compares it with other specimens in major museums. The type-specimens of all nominal species, except one, have been reexamined.

MATERIALS AND METHODS

The material here discussed mainly results from recent collecting work on Sri Lanka. (AL, CG and F numbers; when these follow the designation of another museum, the specimen has already been deposited there.) Locality and elevational data are available for these specimens. The latter datum is important as these species occupy extremely steeply sloping hill sides and town and local settlement names by themselves are insufficient for determination of elevation. (We borrowed only some museum specimens, emphasizing those that had specific localities, beyond that of country. However, under Locality Records, we list, in brackets, all those records noted in the literature and in museum collections of which we are aware. Some specimens in various collections were examined after this report had been completed. Their numbers are preceded by an asterisk (*) under Locality Records, but their counts are generally omitted from the tables.) Catalog numbers for specimens deposited in Sri Lanka are not yet available.

The available data pose some problems relating to the topography of Sri Lanka. The higher mountain ranges are steep with many hill sides inclined at more than 45 degrees. The altitude of localities separated by only a short distance may differ by 500 m. Consequently, the elevation assigned to specimens must be that at which they were actually collected, rather than that of the nearest settlement. As most such information is available for the recent collections they have been emphasized here.

Most of the previous records pose no problems. However, the elevations given in the literature records for the Namunukula area do. The elevations of several of the estates within a few kilometers of the town range from 400 to near 1500 m. While *A. brachyrrhos* and *A. trachyprocta* may be sympatric here, the recent collections indicate that the zone of sympatry is much narrower than that suggested by the collections now in the British Museum.

Material from the following museums was available for comparison. We thank the curators, names in parentheses, who facilitated the loans.

AL—Field number, Carl Gans collection.

AMNH—American Museum of Natural History, New York (R. G. Zweifel).

ANSP—The Academy of Natural Sciences at Philadelphia, Pennsylvania (M. A. MacFarlane and T. M. Uzzell).

BM—British Museum (Natural History), London (A. G. C. Grandison and E. N. Arnold).

BNHM—Bombay Natural History Society, Bombay, India (J. C. Daniel).

CG—Carl Gans collection, Ann Arbor, Michigan.

CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (C. J. McCoy).

F—Field number Carl Gans collection.

FMNH—Field Museum of Natural History, Chicago, Illinois (H. K. Voris).

KU—Museum of Natural History, The University of Kansas, Lawrence, Kansas (W. E. Duellman).

MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts (J. P. Rosado).

MHNP—Museum National d'Histoire Naturelle, Paris, France (R. Roux-Estève).

NHMB—Naturhistorisches Museum zu Basel, Switzerland (U. Rahm).

NMSL—National Museum, Colombo, Sri Lanka (R. Ratnapala and P. H. D. H. de Silva). [This museum now appears to have only *A. trachyprocta*, though the catalog lists other species as well.]

USNM—United States National Museum, Washington, D.C. (G. Zug).

ZMB—Zoologisches Museum, Berlin, D. D. R. (Specimens kindly checked by Dr. G. Peters).

ZMH—Zoologisches Museum, Hamburg, F. D. R. (H. W. Koepke).

ZSI—Zoological Survey of India, Calcutta, India (K. K. Tiwari).

Characters initially examined for each specimen include the numbers of ventrals, subcaudals, and dorsal scale rows, the head scalation pattern, and the color pattern. The various characters were determined as follows:

Sex.—Some specimens were sexed through a midventral incision anterior to the cloaca, by noting the presence of ovaries and oviducts or testes and associated ducts. In some cases the base of the tail was also cut to detect the hemipenes or scent glands. When the distribution of a meristic character suggested a bimodal pattern, a number of animals were selected for sexing; however, only about 20% of the total number of specimens were sexed.

Ventral scales.—Ventrals were counted from the first scale adjacent to the posterior pair of chin shields, up to, but not including the anal plate. The number of narrow anterior ventrals, flanked on each side by an extra dorsal row, was also noted. These latter scales are not to be confused with the additional scale rows that some species show more dorsally. The 75% error bounds for the mean number of ventral scales and subcaudal scales were calculated based on Chebyshev's inequality (mean ± 2 standard error of the mean), which is independent of the distribution of the population being sampled (Schaeffer et al., 1979). These error bounds are included in the species diagnoses.

Subcaudal scales.—The subcaudals were examined to note which were azygous and which divided. Subcaudals were counted from the first scale posterior to the cloacal slit up to the scales immediately preceding the terminal spine.

Dorsal scale rows.—The dorsal scale rows were counted diagonally across the back in the neck region (near ventral 10), at mid-body, and in the precloacal region. When additional scale rows occurred in the nuchal region (as in *A. trachyprocta*), the anterior count was made posterior to their point of termination, although the presence of additional rows was noted. Some specimens (of *A. trachyprocta*) have portions of the second and third scale rows variably fused in the cloacal region. Such fusions were uncommon, and the number of precloacal rows of dorsal scales was determined in regions in which no fusion was noted.

Snout-vent length.—Snout-vent length was measured by pressing the snake against a meter stick. Repeated measurements of the same snake agreed within $\pm 2\%$.

Tail length.—Tail length was measured from the posterior edge of the scale preceding the anal plate to the tip of the tail.

Head scalation.—The number, relative sizes, and pattern of head scales on each snake were examined under a dissecting scope. Particular features useful in distinguishing among species included the presence or absence of a preocular, the relative size of the two postoculars, the number of postoculars contacting the parietal, and contact or lack of contact between prefrontal and orbit. The maximum linear dimension of the postocular was measured.

Color patterns.—The ground color of the dorsal and ventral regions were noted, as were the array of scale markings, their size and distribution.

GENERIC ASSIGNMENT

The head scalation and general habitus easily distinguish the small snakes of the genus *Aspidura* from all other forms in Sri Lanka, except

for the monotypic *Haplocercus ceylonensis*. The latter differs from known species of *Aspidura* (see Smith, 1943; Deraniyagala, 1955) in having higher numbers of ventrals (more than 160 rather than fewer than 161) and caudals (more than 37, rather than fewer than 36, except for one specimen of *A. brachyorrhos*, MCZ 39818), by fusion of the nasal with the first supralabial, by a blunter snout, and by much lower numbers (10 to 12, rather than more than 20) of subequal maxillary teeth.

The somewhat larger Indian species *Blythia reticulata*, *Xylophis perroteti*, and *X. stenorhynchus* also are superficially similar to species of *Aspidura*. *Blythia* may be differentiated by the paired anal plate; the species of *Xylophis* by their loreal scales and contact between mental and chin shields. All three have paired internasals.

The head of *Aspidura* is not distinct from the neck and the cylindrical body gradually increases in diameter to the third quarter and then gradually diminishes, more sharply posterior to the cloaca and on the short tail. The nostril is enclosed by two nasals that lie dorsal and lateral to it and by the ventrally positioned first supralabial. There are six supralabials and six infralabials. The fourth supralabial always forms the ventral border of the orbit. The single median internasal is diamond-shaped and contacts the rostral and nasals anteriorly and the prefrontal posteriorly. The frontol is in broad contact with the supraocular. There is no loreal, but there may be a preocular; two postoculars are the rule, although they may rarely be fused. The elongate parietals are the largest scales on the head; laterally they are flanked by one first and two elongate second temporals on each side. The mental scale is about three times as wide as long, and the medially-contacting first infralabials are followed by two (three in the holotype of *A. copei*) pairs of elongate chin shields. The ventrals are rounded. The scales of the trunk are smooth and lack apical pores; the lateral scales in the cloacal region of some species may be spinose.

Less obvious characteristics mentioned by Smith (1943) are the tendency to have subelliptical rather than round pupils, the occurrence of hypapophyses throughout the vertebral column, and the presence of hemipenes similar to those of *Trachischium*.

MAJOR GROUPINGS

Examination of the available specimens revealed variability in such characters as counts of ventrals and subcaudals, and to a lesser extent color pattern. However, it was possible to characterize six groups of snakes based on (1) the number of scale rows at midbody, (2) presence or absence of a preocular scale, (3) contact (or lack of contact) between prefrontal and orbit, (4) number of postoculars contacted by the pa-

rietal, (5) the relative length of the upper and lower postoculars, and (6) the condition (single or divided) of the subcaudal scales.

The six groups (Table 1) and their ranges are as follows (Localities in parentheses are those of specimens from museum collections obtained on loan; we also list in parentheses the names ultimately assigned to the taxa.):

The first group (*A. brachyorrhos*) is widely distributed (Fig. 1) with new records (museum specimens in parentheses) from Devatura Rd. near Namunukula, (Dimbulla), Gammaduwa, Gampola, Hali Ela, Kandy, (Matale), (Medamaha Nuwara), (Monaragala), (Namunukula), Pallatenne (Peradeniya), (Pundaluoya), and Weligalla. All sites (except the museum records for Namunukula, which refers to a trading center amid a very steep tea-planted mountainside ranging from 300 to above 1400 m, and Pundaluoya at 1230 m) are between 350 and 900 m in elevation.

The second group (*A. copei*) was not included in the collection. Only the "no locality" holotype and six other specimens are available.

The third group (*A. drummondhayi*) is recorded on the basis of a single specimen taken above Deniyaya (Sinharaja Army Camp, nr. 1040 m). Other records (Balangoda) are also from the southwestern portion of Sri Lanka.

The fourth group (*A. guentheri*) is recorded from Deniyaya, Kandilpana, Ratnapura, (Rosagalla ?), (Yala National Park), and Yapitika (nr. Deniyaya), all lowland forest localities in the southern portion of Sri Lanka.

The fifth group (*A. trachyprocta*) is recorded from localities in the central mountain region, over a wide range, generally above 750 m. Localities are Ambawela, (Bopatalawa), Eskdale, Gammaduwa, Harasbedda, (Horton Plains), Kanawarella, (Kurnbakkan ?), Labukelle, Langton Estate, (Maha Eliya), (Medamaha Nuwara), (Moneragala), (Namunukula), (Nanu Oya), Nuwara Eliya, (Ohiya), Pattipola, Pindarawatta, (Pundaluoya), Sita Eliya, and (Talawakele).

The sixth group (*A. deraniyagalae*) is known only from Kanawarella, Pindarawatta, and the Spring Valley Road, all above Namunukula at high (1000 m+) elevation sites on the southeastern portion of the central mountains.

The ranges of the groups differ markedly in size and overlap. Group 5 ranges widely over the central mountains at high elevations; its seeming sympatry with group 1 over a wide area breaks down when one notes that the latter is generally obtained at lower elevations. While the ranges of groups 3 and 4 suggest that they occur at adjacent localities in the southwestern portion of the island, the record for group 3 is again for a higher elevation. Little can be stated about group 2, as only one specimen bears locality data and another locality (referring

Table 1.—Summary of the pattern of characters for the six species of *Aspidura*.

Characters	<i>brachyorthos</i>	<i>copei</i>	<i>deraniyagalae</i>	<i>drummondhayi</i>	<i>guentheri</i>	<i>trachyprocta</i>
Dorsal scale rows	17	17	17	15	17	15
Preoculars	present	absent	present	absent	present	present
Prefrontals	excluded from orbit	contacts orbit	contacts orbit	contacts orbit	contacts orbit	contacts orbit
Number of postoculars touching parietal	2	2	2	2	1 (upper)	2
Largest postocular	lower	lower	lower	lower	upper or subequal	lower
Number of ventrals	146.07 \pm 2.58	129.14 \pm 3.36	119.92 \pm .73	113, 118, 119	112.48 \pm 2.53	137.66 \pm .84
Number of subcaudals	31.37 \pm 1.27	24 \pm 6.93	17.77 \pm 2.82	18, 18, 26	22.35 \pm 1.12	18.70 \pm .74

to a district) is suspect and documented only by a skull. Finally there is group 6, a series of which were collected from the same locality as a series of group 5.

VARIATION OF OTHER CHARACTERS

Basis

The states of other characters of members of the six groups thus defined were examined to determine how many of them supported these groupings (Table 1). The possibility that the groups could be further subdivided on the basis of these characters was also examined. No grounds for further subdivision were found. The intergroup differences in these characters are discussed below.

Sexual Dimorphism

Sexual dimorphism was noted in several characters of most groups (the sample size for *A. drummondhayi* [3] was too small to arrive at a decision). Dimorphism is expressed by absolutely larger females which may have a greater number of ventrals and shorter relative tail length, whereas males may have a greater number of subcaudals (Tables 2). Group 1 (*A. brachyorrhos*) is the only one in which the ventrals show clear-cut sexual dimorphism. Although ventral counts may show some sexual dimorphism in group 5 (*A. trachyprocta*), male and female ranges overlap substantially. Group 1 (*A. brachyorrhos*) shows some sexual dimorphism in the number of subcaudals, while the values for groups 2, 4, 5 and 6 (*A. copei*, *A. guentheri*, *A. trachyprocta*, and *A. deraniyagalae*) suggest clear cut dimorphism in this character. The data from the specimens sexed suggest that females have relatively shorter tails in all groups. They also suggest that in all groups, except 5 (*A. trachyprocta*), the females are larger; in the latter group there is no sexual dimorphism in body length. The variably expressed spines on the lateral scales of the cloacal region of some species are more obvious in males.

Numbers of Ventrals (Fig. 2)

Fig. 2 shows the numbers of ventrals for the six groups. It indicates that the ranking of groups is 4, 3, 6, 2, 5, 1 (*A. guentheri*, *A. drummondhayi*, *A. deraniyagalae*, *A. copei*, *A. trachyprocta*, and *A. brachyorrhos*) in order of increasing number of ventral scales. While there may be differences in the means for the available specimens of each group, the ranges of the first three overlap broadly, as do those of the last three. More substantial differences in ventral counts are found if only males or females are separated for comparison among groups.

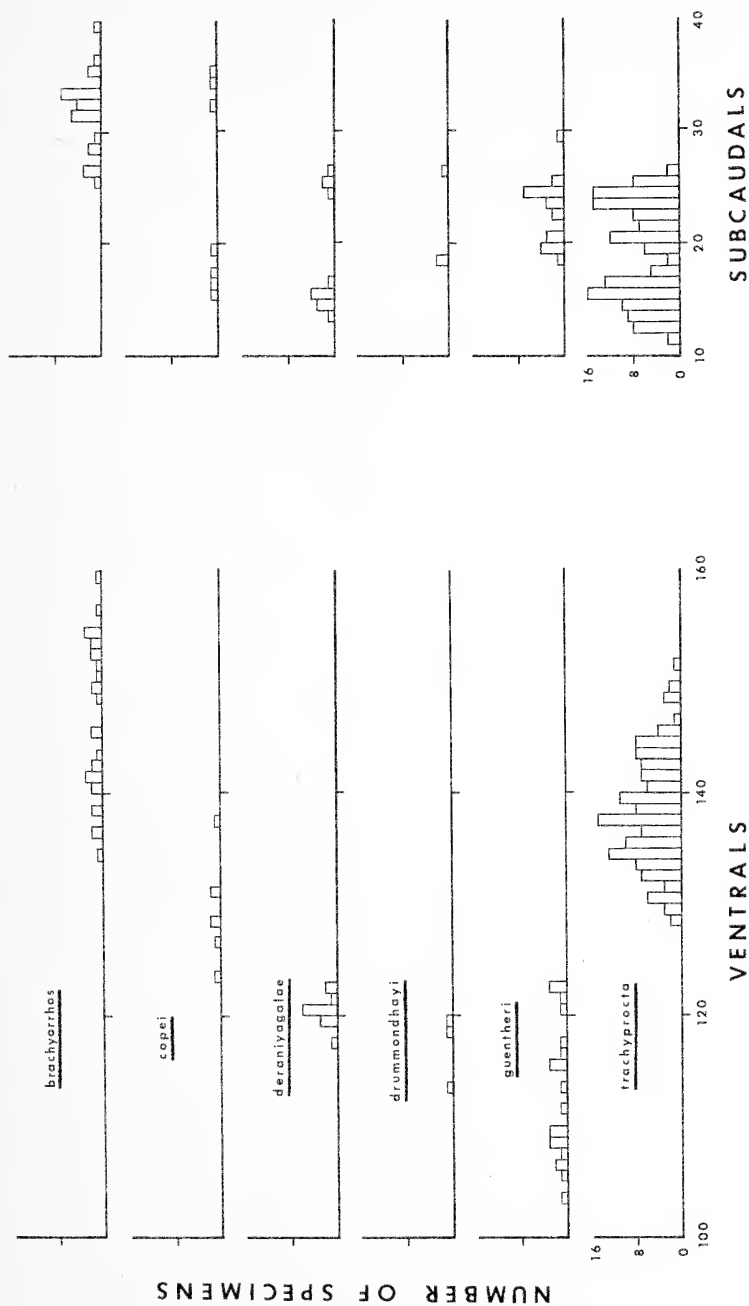


Fig. 2.—Frequency histogram of the number of ventrals (left) and subcaudals (right) for the specimens of *Aspidura* examined. From top to bottom: *A. brachyorrhos*, *A. copei*, *A. deraniyagalae*, *A. drummondhayi*, *A. guentheri*, *A. trachyprocta*. Maximum vertical value equals 16, horizontal divisions equal to one.

Numbers of Subcaudals (Fig. 2)

Groups 6, 3, and 5 (*A. deraniyagalae*, *A. drummondhayi*, and *A. trachyprocta*) have the lowest numbers of subcaudals; group 4 (*A. guentheri*) has slightly more. Groups 1 and 2 (*A. brachyorrhos* and *A. copei*) have somewhat higher counts; however, the figure illustrates substantial overlap among groups with females of group 2 (*A. copei*) having much lower numbers of subcaudals than males. The male and female samples occupy the higher and lower portions of the ranges, respectively, for each of the groups. The differences among groups become more obvious when the sexes are compared separately.

Cloacal Spines

In group 5 (*A. trachyprocta*) the lateral scales of the cloacal region usually bear obvious spines. In groups 1, 2, 3, and 6 (*A. brachyorrhos*, *A. copei*, *A. drummondhayi*, and *A. deraniyagalae*) there is some evidence of spines. In group 4 (*A. guentheri*) spines are absent.

Body Proportions (Fig. 3)

The groups show marked differences in body length. Group 4 (*A. guentheri*) is by far the shortest, followed by groups 6 and 3 (*A. deraniyagalae* and *A. drummondhayi*). Groups 1 and 5 (*A. brachyorrhos* and *A. trachyprocta*) are substantially longer, with the latter showing a few larger individuals than the former. Group 2 (*A. copei*) is apparently the longest (and stoutest) based on the available specimens and literature records (Müller, 1887; Willey, 1906; Wall, 1923a).

The analysis of body diameter is complicated by such conditions as the presence of food in the gut and nutritional state; also, the body diameter increases during pregnancy. However, one can discern some slight intergroup differences in body diameter. Group 4 (*A. guentheri*) specimens are clearly more slender than those of group 6 (*A. deraniyagalae*) and perhaps group 3 (*A. drummondhayi*). Even adult specimens of group 4 (*A. guentheri*) show almost no overlap in size with specimens of groups 1 (*A. brachyorrhos*) and 3 (*A. drummondhayi*). The large sample of group 5 (*A. trachyprocta*) shows great variability and overlaps the ranges of the other groups.

While tail length shows considerable variability, the tails of groups 1 (*A. brachyorrhos*) and 2 (*A. copei*) appear relatively longer than those of the other groups.

Color Pattern

The coloration is highly variable. There is never any concordance between color pattern and scale pattern. The ground colors are shades

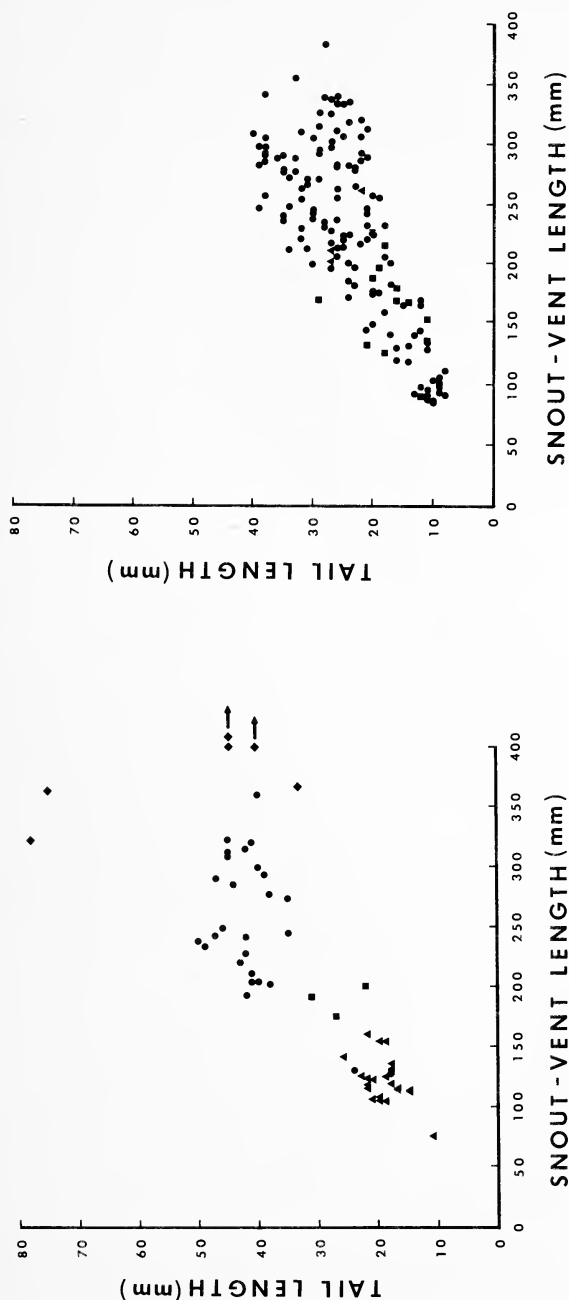


Fig. 3.—Scatter diagrams of snout vent length (abscissa) versus tail length (ordinate) of six species of *Aspidura*. Left figure for *A. quentheri* (triangle), *A. drummondhayi* (square), *A. brachyrrhos* (dot), *A. copei* (diamond). Right figure for *A. deraniyagala* (square) and *A. trachyprocta* (single specimen, dot; two specimens, triangle). The arrows adjacent to diamonds indicate large specimens of *A. copei* with snout vent lengths greater than 400 mm. The two specimens with tail lengths of 45 mm have snout vent lengths of 430 mm and 524 mm. The specimen with a tail length of 40 mm has a snout vent length of 450 mm.

of beige, dark brown, or light tan, all appearing mottled under the dissecting microscope. The head often shows a stripe that parallels the canthus rostralis. Groups 1, 2, and 4 (*A. brachyrrhos*, *A. copei*, and *A. guentheri*) have a light collar extending down the side of the head behind the eye.

When the dorsal color is light enough, a series of dorsal spots may be visible; these occur as a single vertebral row, a pair of rows, one on each side of the midline or a combination of these. Such spots often fuse into a single stripe at the level of the cloaca which extends onto the tail. These dorsal spots are generally about the size of one scale except in group 2 (*A. copei*), in which their area is that of approximately four scales. In groups 1, 2, 4, and 6 (*A. brachyrrhos*, *A. copei*, *A. guentheri*, and *A. deraniyagalae*), the area anterior and posterior to the spots is countershaded by light markings. Specimens of groups 3 and 6 (*A. drummondhayi* and *A. deraniyagalae*) may have a one scale wide vertebral stripe. Groups 3, 5, and 6 (*A. drummondhayi*, *A. trachyprocta*, and *A. deraniyagalae*) have lateral stripes also approximately one scale wide; these stripes are normally arranged between the second and third rows of dorsals on each side and extend from the region of the neck onto the tail, where they tend to lie one scale row above the subcaudals.

The ventral surface may show a suffused even color or a mossy blotching (that is, the pigmentation will then be produced by very large melanocytes, the processes of which are most obvious when the cells are dispersed on a lighter background). The ventral surface may also show very irregular, bold blotches that are generally placed midventrally. The pigmentation is almost always darker posteriorly and darkest on the ventral surface of the tail.

RELATIONSHIPS OF THE GROUPS

Group 2 (*A. copei*) is clearly distinct from the other groups. While there are few acceptable locality data, the animals in group 2 are much larger (Fig. 3 and Willey, 1906; Wall, 1923a) and show a color pattern of large bold spots that is strikingly distinct from that of all other groups. Four specimens of group 2 (Boulenger, 1904, now represented only by a skull in the BM) had the same locality label as the type-specimen of group 3 (*A. drummondhayi*), further supporting recognition of group 2 as a distinct species.

A second discrete assemblage is group 4 (*A. guentheri*), known from lowland forest localities in the southern portion of the island. Reliable literature records document the occurrence of the group in southeastern forests. Early literature comments about a restriction to coastal localities are in error. The animals are far smaller than are those of the other species and differ from all other forms in having a more wedge-

shaped and pointed head. They are also unique in their uniform beige ventral color and the sharply defined nuchal band.

The next assemblage is group 3 (*A. drummondhayi*) from the southern highlands (800+ m), which on the basis of available data is allopatric to all forms except group 2 (*A. copei*) (Boulenger, 1904). Its range adjoins the range of group 4 (*A. guentheri*) near Deniyaya.

Groups 1, 5, and 6 (*A. brachyorrhos*, *A. trachyprocta*, and *A. deraniyagalae*) are sympatric or parapatric in various combinations. Group 1 (*A. brachyorrhos*) ranges from Gammaduwa in the north to the vicinity of Namunukula in the south. All documented specimens were taken between 350 and 900 m (with the exception of two localities documented by museum specimens). Group 5 (*A. trachyprocta*) occurs between 750 and 2100 m and is sympatric with group 1 (*A. brachyorrhos*) at Gammaduwa, Namunukula, and Pundaluoya. The third assemblage is group 6 (*A. deraniyagalae*), known only from localities above 1000 m at Namunukula, at one of which it is definitely sympatric with group 5 (*A. trachyprocta*).

Group 1 (*A. brachyorrhos*) is clearly distinct from groups 5 (*A. trachyprocta*) and 6 (*A. deraniyagalae*) in numerous morphologic characters. Group 1 has the highest number of ventrals and of caudals and is the only species showing sexual dimorphism in the former character. Its color pattern is much lighter than that of the other two and shows a distinct single row of vertebral spots. These color pattern characteristics also serve to distinguish group 1 from the allopatric group 3 (*A. drummondhayi*).

A decision about the relationships of groups 5 (*A. trachyprocta*) and 6 (*A. deraniyagalae*) and perhaps group 3 (*A. drummondhayi*) is necessary. Groups 3 and 5 are apparently allopatric. However, the intermediate zone has been inadequately collected. Group 3 is more uniformly darkly pigmented, with a dorsal stripe instead of the spots usually present in group 5. While members of group 5 may be as dark as group 3, they always retain a light-colored, rather than a dark ventral surface. The numbers of ventrals and subcaudals are similar. Group 3 lacks a preocular, which is present in group 5. The subcaudals are divided in group 3 and azygous in group 5. These scale characteristics are constant and do not vary within either group. In the absence of clearly intermediate specimens, these two groups are retained as distinct species.

Finally there is group 6, sympatric with group 5 near Namunukula where the latter reaches the lower portion of its elevational range. They differ from each other in the number of dorsal scale rows (5, 15; 6, 17), in the division of the subcaudals (5, azygous; 6, divided), in body proportions (5, larger; 6, smaller, Fig. 3) and in number of ventrals (5, 128 to 151; 6, 117 to 122). The pigmentation is superficially

similar with respect to the lateral stripes, the dorsal stripe on the tail, and head pigmentation, but group 6 differs in the more regular and parallel arrangement of two instead of three rows of dorsal spots which usually flank a broken middorsal stripe, and in its lighter dorsal ground color. The samples from the region of sympatry or parapatry are adequate and none of the specimens shows intermediacy.

Groups 3 (*A. drummondhayi*) and 6 (*A. deraniyagalae*), while easily identifiable, show substantial similarity in meristic characters. Groups 5 (*A. deraniyagalae*) and 6 (*A. trachyprocta*) are most similar in coloration.

The five groups for which we have acceptable locality data are either allopatric, or if parapatric their ranges overlap narrowly and are separated altitudinally in the zone of overlap. The most widely ranging groups are regularly observed in the tea plantations that extend over much of the mountain ranges and the eggs of *Aspidura* have been found in open areas immediately adjacent to zones of tea bushes. In some such areas the snakes prove to be extremely common. For example, one open zone just below Ambawela Station produced twenty-seven specimens during one hour and a half of collecting with the aid of three tea workers.

All of this suggests that local sympatry of several species may be a recent phenomenon in species that have become associated with open tea areas. There is a possibility that ranges have shifted in time as some of the older literature records show greater range overlap between species than do present records with better documentation. Groups 5 and 6 occupy a zone in the vicinity of Namunukula, that is now almost entirely planted in tea, interrupted only by patches of the original forest along some hill crests, and small grassy areas beneath cliffs and around the gardens adjacent to workers' dwellings. The region around Namunukula has also produced a number of specimens of *Haplocercus ceylonensis* (which is remarkably similar to *Aspidura*) and of two species of uropeltids. Thus long term tropical monoculture of tea bushes seems to support a substantial number and species diversity of snakes feeding on earthworms and invertebrates.

ATTRIBUTION OF NAMES

The oldest available name is *Scytale brachyorrhos* Boie (1827:517) based on plate 22 (25 *per* Schlegel, 1837) of the unpublished manuscript of a "Érpetologie de Java" (Boie, ms, parts still preserved in the Leiden Museum). The description mentions a single frontal, refers to middorsal brown spots on a rust-colored dorsal surface and 143 (145 in Boie, ms) ventrals plus 28 caudals. The form was made the type-species of the new genus *Aspidura* by Wagler (1830). In 1831 Boie (also reprinted in Susanna, 1834) wrote that the type, which had ap-

parently been obtained by a Mr. Drapiez, did not come from Java, but from Ceylon. The 1827 publication did not list the location of the type, but Boie's manuscript notes indicate that it was in the "Mus. Bruxelles," that is, in Brussels (rather than Paris, as assumed by later authors). The holotype appears to have been lost, as there are no records in Brussels or Tervuren, but the description and illustration of head scales including mention that the prefrontal was excluded from the orbit fits the diagnosis of our group 1; however, the middorsal spots mentioned in the text are illustrated as a broken middorsal line. The name is here assigned to group 1.

Schlegel (1837:42) noted that "*brachorrhos*" came from the Philippines or Ceylon (see also Duméril and Bibron, 1854), placed it in the genus *Calamaria*, and assigned the new specific name *C. scytale* derived from the generic name. He referred to two specimens assumed by all later authors (see Duméril and Bibron, 1854) to have been the types of *S. brachyorrhos*. These (MHNP 1322, 7214; labelled as from the Philippines and collected by Leschenault) are now in the Paris Natural History Museum and were examined for comparison. They appear to be typical examples of group 1, show the color pattern mentioned in the description and agree with the other characteristics of the form. One specimen (MNHP 1322) has three (rather than two) postoculars on the left side of the head, whereas the other one has only a single postocular on the right. The number of ventral scales of the former specimen agrees well with the original description; however, a portion of its tail appears to have been removed as it only retains 13 subcaudals. The tail of the second specimen also shows damage. The name *scytale* is thus a junior synonym of *brachyorrhos*.

The second name available for the group is *Aspidura trachyprocta* Cope (1860). It was based on a single specimen (ANSP 3308) collected in "Ceylon" by Mr. Cuming (M. Cumming in the catalog). The holotype was examined as part of the present study. The description, which mentions the more uniform dorsal coloration and ventral patching, and notes that the peculiar tuberculation of the "ischadic region" is of assistance to the animals for burrowing in the earth, is in good agreement with the specimen. The faded dorsal color of the type-specimen shows the series of spots typical for this form. The value reported for the ventral count is low, which suggests that the count was not started immediately posterior to the chin shields. The presence of 15 scale rows, undivided subcaudals, and agreement in details of head scalation leave no doubt that this name pertains to group 5.

The third name in the genus is *Aspidura copei* Günther (1864) based on a single specimen (BM 1946.1.12.9) purchased by the British Museum, without locality but assumed to have been obtained from Ceylon. The details of color pattern, scalation, and body proportions in

the description are in good agreement with the type-specimen. The only significant difference is that Günther considered the postorbitals to be subequal, whereas we find the upper to be somewhat smaller. The name appears to pertain to group 2.

The fourth name in the genus is *Aspidura guentheri* Ferguson (1876), which was based on a series of 12 specimens, 11 of which are now in the British Museum (BM 1946.1.12.16–1946.1.12.26) while the twelfth specimen is in the Museum of Comparative Zoology (MCZ 28467). Unfortunately these lack more specific locality than “Ceylon,” though Ferguson in his diagnosis notes that “*A. guentheri* occurs close to the coast and never far from it.” The counts given in the description are in good agreement with the type specimens examined and the name pertains to group 4.

The fifth name in the genus is *Aspidura drummondhayi* Boulenger (1904) based on two specimens (BM 1946.1.12.45–1946.1.12.46, labelled “Hopeville” estate) collected “by H. M. Drummond-Hay during March, April, and May 1903” at elevations between 3500 to 4200 ft on the Hopewell estate, Balangoda, Ceylon. This was the first Sri Lankan *Aspidura* species to be described from a specific locality. The description notes the occurrence of 15 rows of dorsal scales and is in good agreement with the type specimen examined. The name clearly pertains to group 3. This needs to be stressed, as subsequent authors (Smith, 1943; Taylor, 1950) have used the name for specimens with 17 rows without noting that the type-specimens have only 15 rows.

There being no other available names for species of this assemblage, we take pleasure in naming the new species, group 6, for Dr. P. E. P. Deraniyagala.

KEY TO THE SPECIES OF THE GENUS *ASPIDURA* (See Fig. 4)

1. Dorsal scales in 15 rows 2
Dorsal scales in 17 rows 3
2. Preocular present, subcaudals undivided *A. trachyprocta*
Preocular absent, all or some subcaudals divided *A. drummondhayi*
3. Preocular absent *A. copei*
Preocular present 4
4. Posterior subcaudals divided *A. deraniyagalae*.
All subcaudals undivided 5
5. Prefrontal excluded from orbit *A. brachyorrhos*
Prefrontal contacts orbit *A. guentheri*

SYSTEMATIC ACCOUNTS

Aspidura brachyorrhos (Boie)

Scytale brachyorrhos F. Boie, 1827:517 (plate 22 of Boie, ms). Type-locality: “Java” (=Ceylon, per Boie, 1831; Susanna, 1834; here restricted to Sri Lanka). Holotype: Brussels Museum, apparently lost.

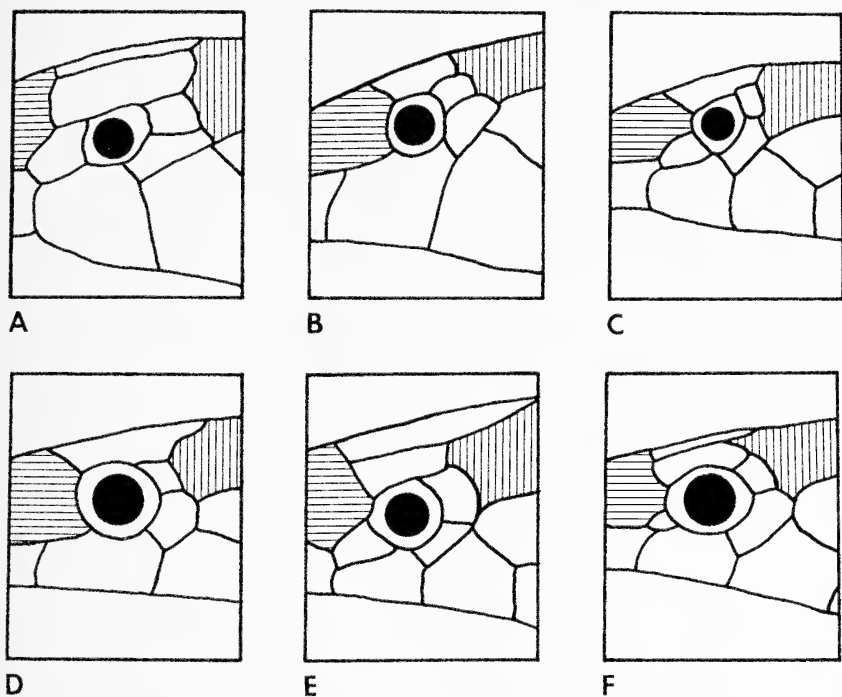


Fig. 4.—A) *Aspidura brachyorrhos*; B) *A. copei*; C) *A. deraniyagalae*; D) *A. drummond-hayi*; E) *A. guentheri*; F) *A. trachyprocta*. Lateral view of head to show the scales around the orbit. Anterior to left. The horizontally hatched scale is the prefrontal and the vertically hatched one the parietal. Other scales shown are the supralabials, preoculars, postoculars, supraoculars, and (sometimes) the frontal.

Calamaria scytale Schlegel, 1837:42. Switch of generic to specific name. Type-locality: Philippines or Ceylon?? Syntypes: MNHP 1322, 7214.

Aspidura brachyorrhos: Taylor, 1953:1620. Erroneous emendation.

Diagnosis.—This species of *Aspidura* is characterized by having a preocular scale; a prefrontal scale that is excluded from the orbit by the preocular scale and contacts supralabials two and three; a lower postocular longer than the upper; both postoculars in contact with the parietal scale; and the anterior pair of chin shields two to three times the length of the posterior pair.

Seventeen dorsal scale rows are present along the body. The ventral counts range from 134 to 159 (mean = 146.07 ± 2.58 , $N = 29$) and those of subcaudals from 25 to 39 (mean = 31.37 ± 1.27 , $N = 27$). The subcaudals are undivided. Snout-vent lengths range from 128 mm to 360 mm, tail lengths from 18 mm to 50 mm, midbody diameters from

4 mm to 9.8 mm (Table 2). Females are larger and have more ventrals than do males. There are no obvious differences in the caudal counts of males and females. Fig. 2 compares the major counts, Fig. 3 the body proportions, and Figs. 5, 8, and 10 illustrate specimens.

Color pattern (preserved specimens).—The ground color is light brown dorsally and a clear, sometimes mottled beige ventrally. The undersurface of the tail is often darkened. None of the pattern elements are sharply defined nor do they correlate with scale geometry. The dorsal surface of the body shows a lightened vertebral stripe about one scale wide in which lie middorsal dark spots approximately five scales apart. A dark stripe runs along each side, from neck to tail, on the level of the second and third dorsal scale rows. In some specimens the stripe also occupies the first dorsal scale row. On the tail it becomes darker and may occupy most of the first and second scale rows. The two dorsal scale rows above the lateral stripe are usually lightened. An irregular, wide (and interrupted) dark neck band is present immediately behind the parietals, and reaches ventrally to the level of the third dorsal row where it is continuous with the lateral stripe.

The snout is covered with variable dark blotches. The side of the head, from rostral, prefrontal, and preocular onto the first temporal, is covered by a zone of dark pigmentation that variably extends toward the lip along the intersupralabial sutures. This lateral dark zone is limited posteriorly by a light zone just posterior to the last supralabials that ascends to the level of the parietals. Posterior extensions of the light zone interrupt the dark nuchal band to form a medial, diamond-shaped blotch flanked by two dark rectangles extending ventrally to the third dorsal row (see Fig. 5). The entire dorsal surface of the snout may be darkened so that the individual blotches are less apparent.

The dorsal ground color appears mottled. The lightened middorsal stripe is discontinuous; being formed by a non-mottled zone lying just anterior and posterior (but not lateral) to the middorsal dark spots. Two lateral rows of dark spots (on dorsal scale row five on each side), not aligned with the middorsal ones, may flank them on the anterior portion of the back.

These spots tend to be irregularly spaced, occur only on some specimens, and fade out posteriorly. The ventral surface may be almost completely pale; however, concentrations of dark pigment may occur along the sutures. In other specimens the ventral pigmentation is much stronger overall with a mossy blotching extending irregularly over the ventral surface. In pale specimens a marked darkening and increase in blotching is present in the subcaudal region. In heavily pigmented specimens the subcaudal zone may be almost completely dark.

Color in life.—Living animals are a rich brown orange with a clear venter (see Gans, 1975:117, for a color photograph of a specimen mis-

Table 2.—Morphological data for six species of *Aspidura* from Sri Lanka. Key to the table is as follows: (M) or (F) after the specimen number indicate male and female, respectively; (A) preocular condition—+ = present, - = absent (right sidelleft side); (B) prefrontal condition—+ = contacting orbit, - = not contacting orbit; (C) relative postocular sizes—+ = upper postocular larger, - = lower postocular larger, 0 = postoculars subequal in size (numbers indicating the number of postoculars replace these symbols where the number of postoculars differs from the usual two); (D) number of postoculars contacting parietal scale (right/left side); (E) subcaudal condition—+ = all subcaudals divided, - = subcaudals undivided, +/- = posterior subcaudals divided; (F) additional dorsal scale rows near head—+, # = present to the ventral scale given, - = absent; (G) cloacal spines—+ = present, - = absent, S = slightly developed, M = medium development, W = well developed.

Museum, catalog nos., and sex	Vent + Caud Scutes	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
<i>Aspidura brachyorrhos</i>										
MNHP 1322	143 + ? (cut)	17/17/17	276 + ? (cut)/6	+/+	-/-	-/3	2/3	-	-	+S
MNHP 7214	152 + 25	17/17/17	360 + 40/8.8	+/+	-/-	1/-	1/2	-	-	-
ANSP 3309	154 + 32	17/17/17	285 + 44/7.7	+/+	-/-	-/-	1/1	-	-	-
CM 83446 (F)	154 + 31	17/17/17	322 + 45/8.5	+/+	-/-	-/-	1/2	-	-	-
CM 83447	159 + 33	17/17/17	128 + 18/4	+/+	-/-	1/1	1/1	-	?	?
MCZ 4236	151 + 33	17/17/17	312 + 45	+/+	-/-	1/1	1/1	-	?	?
MNHP 1331	156 + 32	17/17/17	314 + 42/8.8	+/+	-/-	-/-	2/2	-	-	-
CM 83448 (F)	152 + cut	17/17/17	285 + cut/8.9	+/+	-/-	-/1	2/1	-	-	-
AMNH 120244	154 + 26	17/17/17	277 + 38/9.1	+/+	-/-	-/-	2/2	-	-	-
AL 105a	153 + 26	17/17/17	273 + 35/7	+/+	-/-	-/-	2/2	-	-	-
AL 105b	142 + 32	17/17/17	204 + 40/7	+/+	-/-	-/-	2/2	-	-	+S
CM 83449 (M)	138 + 33	17/17/17	220 + 43/5.9	+/+	-/-	-/-	2/2	-	-	-
AMNH 99392	141 + 35	17/17/17	243 + 47/6	+/+	+/+	-/-	2/2	+/-	-	?
CM 83450 (M)	136 + 36	17/17/17	130 + 24/5.3	+/+	-/-	-/-	2/2	-	-	-
CM 83454 (F)	153 + 28	17/17/17	320 + 41/8.1	+/+	-/-	-/-	2/2	-	-	-
USNM 225075	150 + 29	17/17/17	308 + 45/7.8	+/+	-/-	+/+	1/2	-	-	-
USNM 225076 (M)	141 + 33	17/17/17	204 + 41/7.3	+/+	-/-	-/-	2/2	-	-	-
USNM 225077 (F)	149 + 33	17/17/17	290 + 47/7.2	+/+	-/-	-/-	2/2	-	-	-
FMNH 167005	141 + 35	17/17/17	195 + 42/5.5	+/+	-/-	-/-	2/2	-	-	-
MCZ 39817	148 + 32	?	245 + 35	+/+	-/-	1/-	1/2	?	?	?

Table 2.—Continued.

Museum, catalog nos., and sex	Vent + Caud Scutes	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
MCZ 39818	145 + 39	17/17/17	238 + 50	++	-/-	1/-	1/2	-	?	?
CM 83451 (F)	145 + 28	17/17/17	293 + 39/9.8	++	-/-	-/-	2/1	-	-	-
CM 83452 (M)	138 + 31	17/17/17	202 + 38/7	++	+/+	0/-	2/2	-	-	+S
AMNH 120245 (M)	140 + 31	17/17/17	228 + 42/6.4	++	-/-	-/-	2/2	-	-	-
FMNH 120911	140 + 31	17/17/17	211 + 41/5.7	++	-/-	-/-	2/2	-	-	-
FMNH 178418	149 + 26	17/17/17	296 + 40/9	++	-/-	-/-	2/2	-	-	-
FMNH 125015	142 + 33	17/17/17	248 + 46/8.5	++	-/-	-/-	2/2	-	-	+S
CM 83453 (M)	136 + 31	17/17/17	241 + 42/9.1	++	-/-	-/-	2/2	-	-	+S
FMNH 142405	134 + 33	17/17/17	232 + 49/7	++	-/-	-/-	2/2	-	-	-
<i>Aspidura copei</i>										
BM 1946.1.12.9 (M)	126 + 35	17/17/17	364 + 75/13.5	-/-	+/+	-/-	2/2	-	-	+M
BM 1931.5.13.60 (M)	128 + 32	17/17/17	265 + 7/5.5	-/-	+/+	-/-	2/2	-	-	-
BM 1946.4.29.216 (F)	131 + 19	17/17/17	365 + 33/15	-/-	+/+	-/-	2/2	-	-	-
NMB 928 (F)	128 + 15	17/15/15	430 + 45/15	-/-	+/+	-/-	2/2	+/-	-	-
ZMH R01577	131 + 16	17/17/17	524 + 45/25	-/-	+/+	-/-	2/2	-	-	-
ZMH R01578	123 + 34	17/17/17	325 + 78/12	-/-	+/+	-/-	2/2	-	-	+S
ZMH R01579	137 + 17	17/17/17	450 + 40/15	-/-	+/+	-/-	2/2	-	-	-
<i>Aspidura deraniyagala</i>										
CM 83455 (M)	122 + 25	17/17/17	170 + 29/7.9	++	+/+	-/-	2/2	+/-	-	+M
CM 83456	119 + 13	17/17/17	180 + 16/6.8	++	+/+	-/-	2/2	+/-	-	-
AMNH 120246 (M)	120 + 25	17/17/17	132 + 21/5.3	++	+/+	-/-	2/2	+/-	-	+M
CM 83457 (M)	119 + 26	17/17/17	90 + 12/3.9	++	+/+	-/-	2/2	+/-	-	-
CM 83458 (F)	120 + 16	17/17/17	226 + 20/8.6	++	+/+	-/-	2/2	+/-	-	-
USNM 225091 (F)	120 + 14	17/17/17	154 + 11/7.7	++	+/+	-/-	2/2	+/-	-	-
USNM 225092	117 + 15	17/17/17	136 + 11/6.9	++	+/+	-/-	2/2	+/-	-	-
USNM 225093	119 + 14	17/17/17	168 + 14/7.9	++	+/+	-/-	2/2	+/-	-	-
USNM 225094	122 + 15	17/17/17	169 + 16/10	++	+/+	-/-	2/2	+/-	-	-
CM 83459 (F)	120 + 15	17/17/17	188 + 20/10.7	++	+/+	-/-	2/2	+/-	-	-

Table 2.—Continued.

Museum, catalog nos., and sex	Vent + Caud Scutes	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
CM 83460 (F)	120 + 15	17/17/17	197 + 19/8	+/+	+/+	-/-	2/2	+/-	-	-
CM 83461 (F)	120 + 14	17/17/17	215 + 18/11.5	+/+	+/+	-/-	2/2	+/-	-	-
CM 83462 (M)	121 + 24	17/17/17	126 + 18/6.7	+/+	+/+	-/-	2/2	+/-	-	+S
<i>Aspidura drummondhayi</i>										
BM 1946.1.12.45	113 + 26	15/15/15	175 + 27/6.5	-/-	+/+	-/-	2/2	+/-	+7	+S
BM 1946.1.12.46	118 + 18	15/15/15	192 + 31/6	-/-	+/+	-/-	2/2	+	?	-
CM 83467	119 + 18	15/15/15	200 + 22/7	-/-	+/+	-/-	2/2	+	?	-
<i>Aspidura guentheri</i>										
AMNH 120247 (F)	122 + 23	17/17/17	131 + 18/5	+/+	+/+	+1	1/1	-	-	-
CM 83463 (M)	117 + 29	17/17/17	105 + 20/4.2	+/+	+/+	+/+	1/1	-	-	-
MCZ 15803	108 + 24	17/17/17	125 + 19	+/+	+/+	+/+	1/1	?	?	?
BM 1946.1.12.16	113 + 19	17/17/17	130 + 18/4.7	+/+	+/+	0/0	1/1	-	-	-
BM 1946.1.12.17	105 + 24	17/17/17	115 + 22/4	+/+	+/+	0/0	1/1	-	-	-
BM 1946.1.12.18	108 + 24	17/17/17	122 + 21/4.6	+/+	+/+	0/0	1/1	-	-	-
BM 1946.1.12.19	116 + 19	17/17/17	135 + 18/4.2	+/+	+/+	0/0	1/1	-	-	-
BM 1946.1.12.20	106 + 25	17/16/15	118 + 22/4.2	+/+	+/+	0/+	1/1	-	-	-
BM 1946.1.12.21	108 + 19	17/17/17	114 + 15/3.8	+/+	+/+	0/0	1/1	-	-	-
MCZ 28467	109 + 23	17/17/17	119 + 18	+/+	+/+	+/+	1/1	?	?	?
CM 83464 (M)	109 + 25	17/17/17	125 + 23/4	+/+	+/+	+/+	1/1	+/-	-	-
FMNH 172302	115 + 20	17/17/17	114 + 17/3.5	+/+	+/+	0/0	1/1	-	-	-
FMNH 172303	106 + 24	17/17/17	104 + 19/4.2	+/+	+/+	0/0	1/1	-	-	-
FMNH 172304	115 + 22	17/17/17	115 + 17/3.5	+/+	+/+	0/0	1/1	-	-	-
FMNH 172305	103 + 24	17/17/17	106 + 21/4.0	+/+	+/+	+/+	1/1	-	-	-
FMNH 172306	107 + 24	17/17/17	107 + 20/3.5	+/+	+/+	+/+	1/1	-	-	-
CM 83465	122 + 18	17/17/17	75 + 11/2.8	+/+	+/+	+/+	1/1	-	-	-
CM 83466 (F)	120 + 22	17/17/17	154 + 20/4	+/+	+/+	+/+	1/1	-	-	-
USNM 225078 (F)	122 + 19	17/17/17	154 + 19/5	+/+	+/+	+/+	1/1	-	-	-
USNM 225079 (F)	121 + 20	17/17/17	160 + 22/4	+/+	+/+	+/+	1/1	-	-	-

Table 2.—Continued.

Museum, catalog nos., and sex	Vent + Caud Scutes	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
AMNH 104446	115 + 20	17/17/17	113 + 15/3.8	+/+	+/+	?/?	1/1	—	—	?
MCZ 18053	111 + 24	17/17/17	141 + 26	+/+	+/+	+/+	1/1	?	?	?
MCZ 18054	109 + 23	17/17/17	123 + 22	+/+	+/+	+/+	1/1	?	?	?
<i>Aspidura trachyprocta</i>										
CM 83486	130 + 25	15/15/15	236 + 35/6.7	+/+	+/+	-/-	2/2	—	+15	+W
AMNH 24671	148 + 15	15/15/15	383 + 28/12	+/+	+/+	-/-	2/2	—	+	?
ANSP 3308	141 + 21	15/15/15	214 + 25/8	-/-	+/+	-/-	2/2	—	+9	+M
FMNH 10901	143 + 20	15/15/15	237 + 26/6.5	+/+	+/+	-/-	2/2	—	+8	+W
FMNH 27264	145 + 24	15/15/15	263 + 32/8.2	+/+	+/+	-/-	2/2	—	+9	+W
FMNH 124118	135 + 12	15/15/15	232 + 18/8	+/+	+/+	-/-	2/2	—	+9	+S
FMNH 124119	141 + 19	15/15/15	288 + 33/7.9	+/+	+/+	-/-	2/2	+/-	+9	+W
MCZ 3174	121(?) + 24	15/15/15	?	+/+	+/+	0/0	2/2	+	?	?
MCZ 9304	136 + 24	15/15/15	290 + 35/11	+/+	+/+	-/-	2/2	—	?	?
USNM 19214	142 + 23	15/15/15	89 + 9/3	+/+	+/+	-/-	2/2	—	+	?
USNM 56150	144 + 16	15/15/15	339 + 28/10	+/+	+/+	-/-	2/2	+/-	+	?
CM 83468	137 + 20	15/15/15	95 + 11/4	+/+	+/+	-/-	2/2	—	+9	+S
FMNH 142404	139 + 26	15/15/15	282 + 39/9.8	+/+	+/+	-/-	2/2	—	+7	+W
CM 83536	141 + 15	15/15/15	144 + 12/6.2	+/+	+/+	-/-	2/2	—	+9	—
CM 83537	134 + 14	15/15/15	103 + 10/4.5	+/+	+/+	-/-	2/2	—	+7	—
CM 83538	137 + 23	15/15/15	98 + 12/5	+/+	+/+	-/-	2/2	—	+9	—
CM 83539	139 + 17	15/15/15	132 + 14/4.2	+/+	+/+	-/-	2/2	—	+10	—
USNM 225083	136 + 16	15/15/15	292 + 29/10	+/+	+/+	-/-	2/2	—	+6	+S
USNM 225084	138 + 24	15/15/15	176 + 19/4.8	+/+	+/+	-/-	2/2	—	+9	+M
USNM 225085 (M)	140 + 20	15/15/15	186 + 24/7	+/+	+/+	-/-	2/2	—	+8	+M
USNM 225086	139 + 16	15/15/15	283 + 26/9.6	+/+	+/+	-/-	2/2	—	+9	+S
USNM 225087	138 + 23	15/15/15	213 + 26/5.6	+/+	+/+	-/-	2/2	+	+13	+M
USNM 225088	137 + 24	15/15/15	141 + 17/5	+/+	+/+	-/-	2/2	—	+7	+S
USNM 225089	134 + 15	15/15/15	99 + 9/4.9	+/+	+/+	-/-	2/2	—	+9	+S
USNM 225090	142 + 13	15/15/15	111 + 8/4.9	+/+	+/+	-/-	2/2	—	+6	—

Table 2.—Continued.

Museum, catalog nos., and sex	Vent + Caud Scales	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
CM 83469	132 + 24	15/15/15	248 + 34/7.8	+/+	+/+	-/1	2/1	-	+9	+W
CM 83470	143 + 13	15/15/15	292 + 22/11.8	+/+	+/+	-/-	2/2	-	+9	+S
CM 83471	138 + 21	15/15/15	182 + 23/7.5	+/+	+/+	-/-	2/2	-	+12	+M
AMNH 120248	139 + 23	15/15/15	245 + 30/8.2	+/+	+/+	-/-	2/2	-	+11	+W
CM 83472	134 + 16	15/15/15	105 + 9/4.8	+/+	+/+	1	1	-	+8	-
CM 83473	136 + 16	15/15/15	183 + 17/8	+/+	+/+	-/-	2/2	-	+15	-
CM 83474	137 + 14	15/15/15	100 + 9/4.6	+/+	+/+	+/1	2/1	-	+9	-
CM 83475	134 + 22	15/15/15	242 + 30/7	+/+	+/+	-/-	2/2	-	+5	+W
FMNH 121474	138 + 19	15/15/15	271 + 29/8.5	-/-	+/+	-/-	2/2	-	-	+W
FMNH 121475	137 + 25	15/15/15	298 + 39/9.3	+/+	+/+	-/-	2/2	-	+9	+W
FMNH 121476	139 + 19	15/15/15	271 + 31/8.2	+/+	+/+	-/-	2/2	-	+8	+W
FMNH 121477	Broken	15/15/15	Broken	+/+	+/+	-/-	2/2	-?	+7?	+S
FMNH 121478	137 + 15	15/15/15	282 + 24/8.7	+/+	+/+	-/-	2/2	-	+9	+S
FMNH 121479	144 + 13	15/15/15	325 + 27/9.9	+/+	+/+	-/-	2/2	-	+7	+S
CM 83476	145 + 23	15/15/15	228 + 27/8.3	-/-	+/+	-/-	2/2	-	-	+S
CM 83477	149 + 15	15/15/15	278 + 23/10.1	+/+	+/+	-/-	2/2	-	+6	+S
AMNH 94447	143 + 16	15/15/15	312 + 21/8	+/+	+/+	-/-	2/2	-	+	?
FMNH 131365	141 + 15	15/15/15	201 + 17/6.7	+/+	+/+	1/-	1/2	-	+11	+S
FMNH 131366	139 + 13	15/15/15	302 + 27/10.2	+/+	+/+	-/-	2/2	-	+9	+S
FMNH 131367	137 + 20	15/15/15	197 + 23/6.2	+/+	+/+	-/-	2/2	-	+9	+S
FMNH 131368	135 + 23	15/15/15	297 + 38/8	+/+	+/+	-/-	2/2	-	+9	+W
FMNH 131369	140 + 12	15/15/15	318 + 24/9	+/+	+/+	-/-	2/2	-	?	-
FMNH 131370	143 + 11	15/15/15	306 + 22/8.4	?/?	?/?	-/-	2/2	-	+9	-
F 82 (F)	148 + 16	15/15/15	326 + 29/9.3	+/+	+/+	-/-	1/2	-	+12	+S
F 83	143 + 14	15/15/15	306 + 25/8.2	+/+	+/+	-/-	2/2	-	+6	+S
F 84	143 + 22	15/15/15	341 + 38/10.8	+/+	+/+	-/-	2/2	-	+6	+W
CM 83478	151 + 13	15/15/15	334 + 26/9.1	+/+	+/+	-/-	2/2	-	+6	+S
CM 83479	142 + 11	15/15/15	335 + 24/9	+/+	+/+	-/-	2/2	-	+9	+S
CM 83480	149 + 12	15/15/15	166 + 12/5.2	+/+	+/+	-/-	2/2	-	+6	+S

Table 2.—Continued.

Museum, catalog nos., and sex	Vent + Caud Scutes	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
CM 83481	144 + 20	15/15/15	160 + 18/4.6	+/+	+/+	-/-	2/2	-	+9	+S
CM 83482	144 + 24	15/15/15	241 + 35/7.7	+/+	+/+	-/-	2/2	-	+5	+W
FMNH 121947	139 + 12	15/15/15	340 + 26/10.5	+/+	+/+	-/-	2/2	-	+12	-
FMNH 121948	138 + 24	15/15/15	254 + 32/8	+/+	+/+	-/-	2/2	-	+7	+M
F 90	145 + 15	15/15/15	289 + 21/8.3	+/+	+/+	-/-	2/2	-	+7	-
F 91	148 + 22	15/15/15	272 + 34/10	+/+	+/+	1/1	1/1	-	+6	+W
F 92 (M)	139 + 19	15/15/15	224 + 25/6.4	+/+	+/+	-/-	2/2	-	+6	+W
CM 83487	143 + 16	15/15/15	206 + 18/5.3	+/+	+/+	-/-	2/2	-	+7	+S
CM 83488	144 + 23	15/15/15	279 + 35/8.9	+/+	+/+	-/-	2/2	-	+9	+W
CM 83489	133 + 21	15/15/15	285 + 38/10.4	+/+	+/+	-/-	2/2	-	+8	+W
CM 83490	142 + 20	15/15/15	178 + 20/5.9	+/+	+/+	-/-	2/2	-	+8	+S
CM 83491	139 + 22	15/15/15	211 + 27/6.8	+/+	+/+	-/-	2/2	-	+6	+S
CM 83492	144 + 22	15/15/15	238 + 30/6.8	+/+	+/+	-/-	2/2	-	+6	+M
CM 83493	142 + 20	15/15/15	220 + 25/6.6	+/+	+/+	-/-	2/2	-	+8	+M
CM 83494	140 + 14	15/15/15	265 + 23/8.2	+/+	+/+	-/-	2/2	-	+5	+S
CM 83495	146 + 13	15/15/15	255 + 19/7.6	+/+	+/+	-/-	2/2	-	+11	+S
CM 83496	136 + 23	15/15/15	206 + 26/7	+/+	+/+	-/-	2/2	-	+11	+S
CM 83497	141 + 24	15/15/15	211 + 27/6.5	+/+	+/+	-/-	2/2	-	+16	+W
CM 83498	144 + 15	15/15/15	257 + 20/6.5	+/+	+/+	-/-	2/2	-	+10	+S
CM 83483	139 + 23	15/15/15	276 + 35/11.2	+/+	+/+	-/-	2/2	-	+11	+W
CM 83484	140 + 25	15/15/15	230 + 32/9.4	+/+	+/+	-/-	2/2	-	+7	+W
CM 83485	135 + 23	15/15/15	288 + 36/9.2	+/+	+/+	-/-	2/2	-	+9	+W
CM 83500	134 + 15	15/15/15	262 + 26/8.5	+/+	+/+	-/-	2/2	-	+6	+M
CM 83501	137 + 22	15/15/15	292 + 38/8.6	+/+	+/+	-/-	2/2	-	+7	+W
CM 83502	140 + 21	15/15/15	277 + 33/7.8	+/+	+/+	-/-	2/2	-	+2	+W
CM 83503	136 + 20	15/15/15	231 + 28/7.5	+/+	+/+	-/-	2/2	-	+9	+W
CM 83504	137 + 13	15/15/15	261 + 22/7.8	+/+	+/+	-/-	2/2	-	+9	-
CM 83505	139 + 16	15/15/15	166 + 15/5	+/+	+/+	-/-	2/2	-	+9	+S
CM 83506	143 + 15	15/15/15	261 + 22/10.3	+/+	+/+	-/-	2/2	-	+10	+S

Table 2.—Continued.

Museum, catalog nos., and sex	Vent + Caud Scutes	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
CM 83507	142 + 12	15/15/15	286 + 22/9	+/+	+/+	-/-	2/2	-	+5	+S
AMNH 85082	137 + 23	15/15/15	201 + 24/7	+/+	+/+	-/-	2/2	-	?	?
CM 83499	141 + 12	15/15/15	320 + 22/12.5	+/+	+/+	-/-	2/2	-	+7	+S
AMNH 85081	138 + 16	15/15/15	170 + 12/5.5	+/+	+/+	-/-	2/2	-	+	?
CM 83508 (M)	130 + 24	15/15/15	221 + 32/9.5	+/+	+/+	-/-	2/2	-	+7	+W
AMNH 120249 (M)	130 + 24	15/15/15	213 + 31/9.4	+/+	+/+	-/-	2/2	-	+7	+W
CM 83509	135 + 17	15/15/15	141 + 13/7.5	+/+	+/+	-/-	2/2	-	+6	-
CM 83510 (M)	131 + 25	15/15/15	212 + 34/8.8	+/+	+/+	-/-	2/2	-	+7	+W
CM 83511	128 + 25	15/15/15	196 + 27/8	+/+	+/+	-/-	2/2	-	+8	+W
CM 83512	133 + 14	15/15/15	281 + 26/12	+/+	+/+	-/-	2/2	-	+6	+S
CM 83513	134 + 25	15/15/15	172 + 24/8.6	+/+	+/+	-/-	2/2	-	+10	+S
CM 83514	135 + 17	15/15/15	217 + 22/9.1	+/+	+/+	-/-	2/2	-	+10	+S
CM 83515 (F)	137 + 16	15/15/15	246 + 21/10.6	+/+	+/+	-/-	2/2	-	+8	+S
CM 83516	133 + 16	15/15/15	98 + 9/4.2	+/+	+/+	-/-	2/2	-	+12	-
CM 83517	133 + 21	15/15/15	202 + 27/7.9	+/+	+/+	-/-	2/2	-	+4	+S
CM 83518	130 + 24	15/15/15	120 + 16/5.8	+/+	+/+	-/-	2/2	-	+12	+S
CM 83519 (F)	137 + 18	15/15/15	310 + 32/13.9	+/+	+/+	-/-	2/2	-	+8	+S
CM 83520	135 + 16	15/15/15	315 + 29/11.1	+/+	+/+	3/-	3/2	-	+9	+S
USNM 225080	133 + 25	15/15/15	257 + 38/11.1	+/+	+/+	-/-	2/2	-	+4	+W
USNM 225081	132 + 15	15/15/15	129 + 11/6.8	+/+	+/+	-/-	2/2	-	+9	-
USNM 225082	129 + 23	15/15/15	309 + 40/13.9	+/+	+/+	-/-	2/2	-	+4	+W
CM 83521 (M)	131 + 24	15/15/15	200 + 30/9.9	+/+	+/+	-/-	2/2	-	+9	+W
CM 83522 (F)	134 + 14	15/15/15	255 + 26/11	+/+	+/+	-/-	2/2	-	+4	+S
CM 83523	129 + 26	15/15/15	247 + 39/8.7	+/+	+/+	1/+	1/2	-	+8	+W
CM 83524	132 + 14	15/15/15	232 + 21/9.8	+/+	+/+	-/-	2/2	-	+12	+S
CM 83525	131 + 23	15/15/15	130 + 16/6.4	+/+	+/+	-/-	2/2	-	+12	+S
CM 83533	137 + 12	15/15/15	135 + 11/5.6	+/+	+/+	-/-	2/2	-	+10	+S
CM 83526	130 + 24	15/15/15	150 + 20/6.2	+/+	+/+	-/-	2/2	?	+7	?
CM 83527 (F)	130 + 17	15/15/15	305 + 30/12.4	+/+	+/+	-/-	2/2	-	+7	+S
CM 83528	135 + 18	15/15/15	295 + 29/11	+/+	+/?	-/-	2/2	-	+7	+S

Table 2.—Continued.

Museum, catalog nos., and sex	Vent + Caud Scutes	Head/Mid/Cloac Dorsals	S-V + Caud/Diam Dimensions	A	B	C	D	E	F	G
CM 83529	135 + 17	15/15/15	279 + 27/11	+/+	+/+	-/-	2/2	-	+9	+S
CM 83530 (M)	134 + 22	15/15/15	305 + 38/10	+/+	+/+	-/-	2/2	-	?	+W
CM 83531	133 + 12	15/15/15	333 + 25/11	+/+	+/+	-/-	2/2	-	+10	-
CM 83532 (M)	128 + 25	15/15/15	145 + 21/6.9	+/+	+/+	-/-	2/2	-	+11	+S
AMNH 120250	133 + cut	15/15/15	152 + cut/7	-/-	+/+	-/-	2/2	-	+7	+S
AMNH 120251	135 + cut	15/15/15	294 + cut/12	+/+	+/+	-/-	2/2	-	+7	+S
FMNH 120908	140 + 15	15/15/15	280 + 23/8.5	+/+	+/+	0/-	2/2	-	+8	-
FMNH 120909	132 + 15	15/15/15	225 + 20/8.2	+/+	+/+	-/-	2/2	-	+5	+S
FMNH 120910	145 + 15	15/15/15	255 + 24/9.1	+/+	+/+	1/1	1/1	-	+6	+S
FMNH 120912	138 + 22	15/15/15	293 + 38/9.4	+/+	+/+	-/-	2/2	-	+8	+W
MCZ 34890	138 + 14	15/15/15	93 + 9/3	+/+	+/+	-/-	2/2	-	+10	-
MCZ 34891	137 + 20	15/15/15	85 + 10/3	+/+	+/+	-/-	2/2	-	+7	+S
MCZ 34892	134 + 20	15/15/15	88 + 11/3	+/+	+/+	-/-	2/2	-	+7	+S
MCZ 34893	134 + 24	15/15/15	92 + 13/3	+/+	+/+	-/-	2/2	-	+8	+S
MCZ 34894	133 + 19	15/15/15	90 + 11/3	+/+	+/+	-/-	2/2	-	+7	+S
MCZ 34895	142 + 14	15/15/15	91 + 8/2.5	+/+	+/+	-/-	2/2	-	+11	-
MCZ 34896	135 + 19	15/15/15	86 + 10/3	+/+	+/+	-/-	2/2	-	+8	+S
MCZ 34897	132 + 20	15/15/15	214 + 25/7	+/+	+/+	-/-	2/2	-	+8	+W
MCZ 34898	137 + 23	15/15/15	235 + 28/7.5	+/+	+/+	-/-	2/2	-	+6	+M
MCZ 34899	134 + 21	15/15/15	175 + 20/5	+/+	+/+	1/-	1/2	-	+9	+M
MCZ 34900	129 + 21	15/15/15	119 + 14/4.5	+/+	+/+	-/-	2/2	-	+8	+S
MCZ 34901	134 + 23	15/15/15	202 + 27/7.3	+/+	+/+	-/-	2/2	-	+7	+M
MCZ 34902	132 + 20	15/15/15	218 + 27/7.5	+/+	+/+	-/-	2/2	-	+7	+M
MCZ 34903	136 + 15	15/15/15	221 + 21/7.2	+/+	+/+	-/-	2/2	-	+7	+S
MCZ 34904	134 + 21	15/15/15	266 + 31/9.8	+/+	+/+	-/-	2/2	-	+6	+W
MCZ 34905	132 + 13	15/15/15	242 + 21/7.2	+/+	+/+	1/-	1/2	-	+9	+S
MCZ 34906	144 + 14	15/15/15	311 + 26/8.4	+/+	+/+	-/-	2/2	-	+6	+S
MCZ 34907	136 + 15	15/15/15	355 + 33/10	+/+	+/+	-/-	2/2	+/-	+9	-
MCZ 34908	141 + 13	15/15/15	337 + 27/11.5	+/+	+/+	-/-	2/2	-	+11	+S

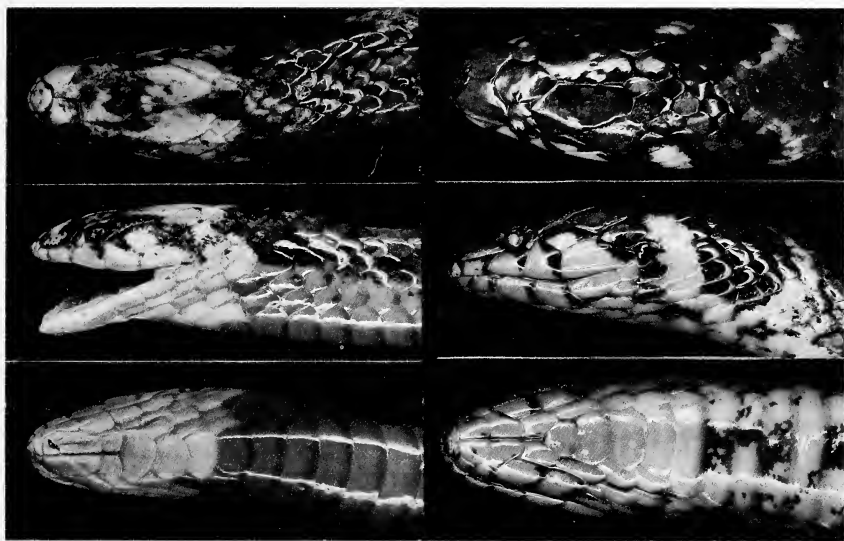


Fig. 5.—Dorsal, lateral, and ventral views of the head of (left) *Aspidura brachyrrhos* (MNHP 7214) and (right) *A. copei* (holotype BM 1946.1.12.9) to show scalation and color pattern.

labelled *A. trachyprocta*). The head is clearly dark brown, and the dorsal spots, neck band, and lateral line are apparent.

Locality records.—SRI LANKA: “Java” (=Ceylon, per F. Boie, 1831; Susanna, 1834), Brussels Museum, apparently lost (holotype of *Scytale brachyrrhos* F. Boie, 1827). “Philippines,” MHNP 1322, 7214 (syntypes of *Calamaria scytale* Schlegel, 1837; Dumeril and Bibron, 1854; Jan, 1862). No specific locality, (Theobald, 1876), ANSP 3309 (Cope, 1860), [Basel Museum, Müller, 1878], [Colombo Museum, Haly, 1886; de Silva, 1972], [Milan Museum, Jan, 1857; Jan and Sordelli, 1865, (13), pl. 2, 2], [“only in the mountains,” Günther, 1858(part); Boulenger, 1890, 1893], CM 83446–83447 (AL 648a–648b), MCZ 4236, MHNP 1331 (Günther, 1864), *ZSI 4423, 7024, 7026, 8390, 8392–8393. Gammaduwa, 750 m, CM 83448 (AL 103a), AMNH 120244 (AL 103b), AL 105a–105b; Pallatenne, 610 m, CM 83449 (AL 530); Matale, AMNH 99392; Weligalla, CM 83450 (AL 637); Kandy district, CM 83454 (AL 638a), *BNHS 1735 (Wall, 1921a); Peradeniya, *BM 1913.2.7.2, *ZMB 7269, *ZSI 16646 (Wall, 1921a); Gampola, 470 m, USNM 225075 (AL 288), USNM 225076 (AL 670b), USNM 225077 (AL 672); 30 mi (= 50 km) east of Colombo, *ZSI 7024 (Sclater, 1891); Medamaha Nuwara, FMNH 167005; Pundaluoya, 4000 ft, *BM 1905.3.25.91; Dimbulla, Queenswood Estate, MCZ 39817–39818; Hali Ela, CM 83451–83452 (AL 548a–548b), AMNH 120245 (AL 548c); Namunukula, Uva, FMNH 120911 (4000 ft, in trench), 178418; Tonacombe estate, Namunukula, *BM 1955.1.9.44–48 (4000 ft), *BM 1968.872 (3500 ft), FMNH 125015, *KU 31253 (is this Kansas Univ. 31238, in Taylor, 1953); Galapitikande, Namunukula, 4000 ft, *BM 1951.1.1.14–15; Devatura Rd. nr. Namunukula, CM 83453 (AL 66); Monaragala, Monaragala estate (3000 ft), FMNH 142405. [Velangoda, Kandy to the Horton Plains, absent from the Valimada (= Welimada?) area, Deraniyagala, 1955]. [Velangoda, Wall, 1921a], [Badulla, Pearless, 1909].

Aspidura copei Günther

Aspidura copei Günther, 1864:203, plate 18E. Type-locality: Unknown, assumed to be "Ceylon." Holotype: BM 1946.1.12.9.

Diagnosis.—This species of *Aspidura* is characterized by the absence of a preocular scale; by a prefrontal scale that forms the entire anterior border of the orbit and contacts supralabials two, three and four; by having the lower postocular longer than the upper; both postoculars in contact with the parietal scale; and by two pairs of chin shields (three in the holotype).

Seventeen dorsal scale rows are present along the body (in NHMB 928 the count drops to 15 near midbody). The ventral counts range from 123 to 137 (mean = 129.14 ± 3.36 , $N = 7$) and those of the subcaudals from 15 to 35 (mean = 24 ± 6.93 , $N = 7$). The subcaudals are undivided. (The Basel specimen has three divided ones.) Snout-vent lengths range from 325 to 524, tail lengths from 33 to 78, and midbody diameter ranges from 5.5 to 25 mm (Table 2). Fig. 2 compares the major counts, Fig. 3 the body proportions, and Figs. 5, 8, and 10 illustrate specimens.

Color pattern (preserved specimens).—This is a boldly-marked species. Its pattern elements do not correlate with scale geometry. A brownish-olive middorsal band two to three scales wide is flanked on each side by a series (23 to 26 spots on each side) of solid dark blotches. Each blotch is two to three scales in width and length, and associated anteriorly and posteriorly with a slightly shorter light region. A brown ground color occupies the area between these light regions and extends ventrally to the second dorsal scale row. The sides of the body show another series of dark markings, each occupying two to four scales. These run into the ventrals and are not visible in dorsal view. The dorsal surface of the head is olive brown. The supra and infralabials are light yellow, with the sutures marked in black. A narrow dark band descends from the temporals, diagonally past the angle of the mouth, to the edge of the ventral surface.

A light middorsal spot marks the first middorsal scale posterior to the parietals. It is flanked by an olive area, ventral to which a narrow (one scale wide) light band extends diagonally posteriorly to join the light ventral region. The light spot is followed posteriorly by a large (three to four scale wide) dark, posteriorly-open V. The ventral arms of the V are darkest and extend to the level of the second dorsal on each side. The posterior edge of the V is lightly countershaded.

The ventral surface of the trunk is mottled. The dark pigmentation is mossy along the sides of the ventral scales and over the entire subcaudal surface. A series of more solidly-pigmented blotches proceeds

along the ventral midline; these are flanked by narrow irregular clear areas. The five most anterior ventral scales are unpigmented.

Under the dissecting microscope the dorsal surface of the snout is a solid olive except for a pair of light spots flanking the dorsal midline along the middle of the parietals. The dark rim of the eye is confluent with the dark band at the posterior end of the fourth supralabial. The first temporal is half black and half light. The ventralmost portions of the dark cephalic markings are much more solidly pigmented than the olive dorsal portions of the head.

Locality records.—SRI LANKA: No locality, BM 1946.1.12.9 (holotype of *A. copei* Günther, 1864; Boulenger, 1893; Theobald, 1876), BM 1931.5.13.60–61, NHMB 928 (Müller, 1887), [Colombo Museum, de Silva, 1972], ZMH R01577–R01579; District of Dimbola (=Dimbula), 4000–5000 ft, *BM 74.4.29.216 (Boulenger, 1890, 1893); [Hopewell Estate, Balangoda, Boulenger, 1904; Smith, 1943; Deraniyagala, 1955]; [Dickoya, Haly, 1886, Boulenger, 1890; Deraniyagala, 1955]; [Avisawella, Willey, 1906; this specimen appears slightly aberrant, and deserves reexamination]. [Pandalu Oya (=Pundaluoya), Deraniyagala, 1955].

Aspidura deraniyagalae, new species

Holotype.—CM 83455 (F 45), a male taken at Kanawarella Group Estate (near Namunukula), at 1520 m, August 1972, by Carl Gans.

Paratypes.—Other specimens listed under locality records; all from the vicinity of Namunukula, and near 1500 m elevation.

Diagnosis.—This species of *Aspidura* is characterized by having a preocular scale that forms a portion of the anterior border of the orbit; a prefrontal scale that forms the remaining portion of the anterior border of the orbit and contacts supralabials two and three; the lower postocular longer than the upper; both postoculars in contact with the parietal scale; and the anterior pair of the two pairs of chin shields one to two times the length of the posterior pair.

Seventeen dorsal scale rows are present along the body. The ventral counts range from 117 to 122 (mean = $119.92 \pm .73$, $N = 13$) and those of subcaudals from 13 to 26 (mean = 17.77 ± 2.82 , $N = 13$). The posterior subcaudals are divided. Snout–vent lengths range from 90 mm to 226 mm, tail lengths from 11 mm to 29 mm, midbody diameters from 3.9 mm to 10.7 mm (Table 2). Females have fewer caudals than males, shorter tails and larger bodies. Fig. 2 compares the major counts, Fig. 3 the body proportions and Figs. 6, 8, and 11 illustrate specimens.

Color pattern (preserved specimens).—The ground color is light beige to darker brown dorsally and blackish brown mottled on a lighter color, ventrally. The under surface of the tail is generally darkened. None of the pattern elements are sharply defined nor do they correlate with scale geometry. The dorsal surface of the body is more or less

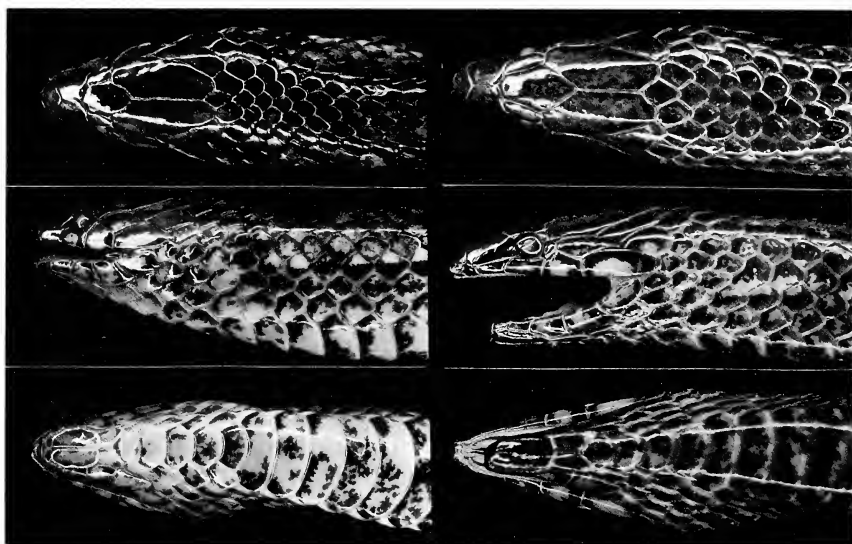


Fig. 6.—Dorsal, lateral, and ventral views of the head of (left) *Aspiderura deraniyagalae* (holotype, CM 83455) and (right) *A. drummondhayi* (syntype BM 1946.1.12.45) to show scalation and color pattern.

uniformly colored; except for two paravertebral rows of dark spots on about dorsal scale row six which usually flank a narrow (less than one scale wide) broken middorsal stripe. Each spot is approximately one scale in size. In dark specimens, these spots are flanked on two sides by lighter regions. A dark stripe is present on the dorsal half of the second and ventral half of the third dorsal scale row on each side of the body. This lateral stripe is flanked dorsally by a half-scale wide light stripe and ventrally by a less distinct light stripe. These lateral stripes extend anteriorly to the level of the seventh ventral and are replaced there by a one to three scale long light area on each side. The dark lateral bands are obvious on the tail to its tip. The blotches flanking the dorsal line terminate at the level of the cloaca and a single dark stripe extends along the dorsal surface of the tail. In light colored specimens, the apex of most of the dorsal scales is more densely pigmented.

The head is fairly heavily and darkly pigmented. The dark regions extend from the rostral through the eye onto the first and second temporals and spread out dorsally and laterally to the light region at the tip of the lateral stripe. The centers of the labial scales and the mid-ventral portion of the first temporal are lightened. A second light area may extend from the lateral aspect of the parietal onto the dorsal

second temporal and first dorsal scales. In some specimens the entire surface of the parietals is mottled with light and dark patches. Usually the middle of the internasal, and the dorsal borders of the prefrontals are lightened. The edges of the infralabials and the first pair of chin shields are darkened; thereafter pigmentation on the ventral surface of the head is irregularly blotched. The ventral surface of the body tends to be most heavily, though irregularly, pigmented along the midline. This darkened zone is flanked on each side by lighter regions and these in turn by darker ones.

Locality records.—SRI LANKA: Kanawarella Group (above Namunukula), 1520 m, CM 83455 (F 45, holotype), CM 83456 (F 50); Spring Valley road (above Namunukula), 1540 m, AMNH 120246 (F64), CM 83457 (F65); above Namunukula, 1520 m, CM 83458 (AL 35b), USNM 225091–225094 (AL 75a–75b, 75d–75e); Pindarawatta (west of Namunukula), 1520 m, CM 83459–83462 (AL 167a–167d).

Aspidura drummondhayi Boulenger

Aspidura drummondhayi Boulenger, 1904:95–96, plus one plate. Type locality: “Hopewell estate, Balangoda, . . . while clearing out drains in a field at the very top of the estate, the probable elevation being from 3500 to 4200 feet above sea level.” Syntypes: BM 1946.1.12.45–1946.1.12.46.

Aspidura drummond-hayi: Smith, 1943:338. Inappropriate emendation.

Diagnosis.—This species of *Aspidura* is characterized by the absence of a preocular scale; a prefrontal scale that forms the entire anterior border of the orbit and contacts supralabials two, three and four; having a lower postocular longer than the upper; both postoculars in contact with the parietal scale; and the anterior pair of the two pairs of chin shields one to two times the length of the posterior pair.

Fifteen dorsal scale rows are present along the body. The ventral counts are 113 to 119 and the subcaudal ones 18 to 26. Either all the subcaudals are divided, or only the posterior subcaudals are divided. Snout–vent lengths are 175 to 200 mm, tail lengths are 22 to 31 mm, midbody diameters are 6.0 to 7.0 mm (Table 2). Fig. 2 compares the major counts, Fig. 3 the body proportions and Figs. 6, 9, and 11 illustrate specimens.

Color pattern (preserved specimens).—The ground color is a rich chocolate brown dorsally and a slightly lighter brown ventrally. While there are traces of stripes and spots, these are not obvious to the unaided eye.

The snout is very dark up to the level of the eye. The dark region extends onto the temporals and the lateral edges of the parietals. The frontal and the rest of the parietals are slightly lighter than the snout. The more posterior supralabials show lightened centers, as do the first temporals and a number of lower dorsals on each side. The pigmentation of the dorsal ground color shows some faint mottling on indi-

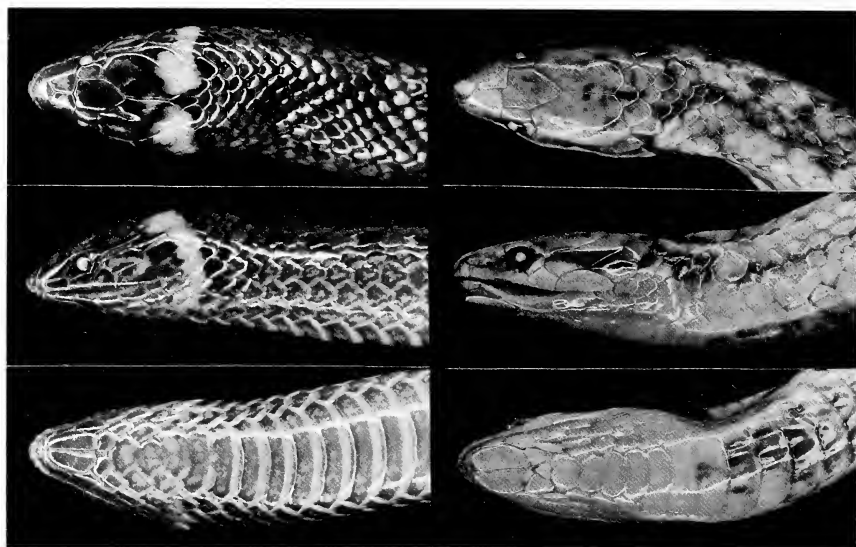


Fig. 7.—Dorsal, lateral, and ventral views of the head of (left) *Aspidura guentheri* (syntype BM 1946.1.12.16) and (right) *A. trachyprocta* (holotype ANSP 3308) to show scalation and color pattern.

vidual scales. The scales are iridescent. A darker middorsal scale row produces a one scale wide vertebral stripe that extends from the parietals to the tip of the tail. The middorsal scales appear darker because of a concentration of brown pigment in an anterior-posterior band across the center of the individual scales. There is a faint dark stripe on the fifth dorsal scale row on each side of the body. A more obvious lateral stripe occurs on the third dorsal scale row on each side. At the level of the vent it drops ventrally and continues to the tip of the tail above the first dorsal scale row on each side.

Under the dissecting scope the ventral pattern appears mottled anteriorly. At the level of about the twelfth ventral the ventral pigmentation is solid, and continues thus to the cloacal scale, the free edge of which is lightened. The ventral surface of the tail is solid brown.

Locality records.—SRI LANKA: Hopewell estate, Balangoda, 3500 ft–4200 ft, BM 1946.1.2.45–46 (syntypes of *A. drummondhayi* Boulenger, 1904; Deraniyagala, 1955); Balangoda Dist., *BM 1931.5.13.58–59; Sinharaja Army Camp, above Deniyaya, 1040 m, CM 83467 (CG 092519B).

Aspidura guentheri Ferguson

Aspidura guentheri Ferguson, 1876:819–820. Type-locality: “Ceylon, . . . close to the coast, and never far from it.” Syntypes: BM 1946.1.12.16–1946.1.12.26; MCZ 28467.

Diagnosis.—This species of *Aspidura* is characterized by a preocular scale that forms part of the anterior border of the orbit; a prefrontal scale that forms the remaining portion of the anterior border of the orbit and contacts supralabials two and three; having the upper postocular longer than the lower or both subequal in length; only the upper postocular in contact with the parietal scale; and the anterior pair of the two pairs of chin shields two to three times the length of the posterior pair.

Seventeen dorsal scale rows are present along the body. The ventral counts range from 103 to 122 (mean = 112.48 ± 2.53 , $N = 23$) and those of subcaudals from 18 to 29 (mean = 22.35 ± 1.12 , $N = 23$). The subcaudals are undivided. Snout-vent lengths range from 75 mm to 160 mm, tail lengths from 11 mm to 26 mm, midbody diameters from 2.8 mm to 5.0 mm, making this the smallest and most slender species of the genus (Table 2). Females have fewer caudals and a shorter tail than males, but are larger overall. Fig. 2 compares the major counts, Fig. 3 the body proportions and Figs. 7, 9, and 12 illustrate specimens.

Color pattern (preserved specimens).—These are slender brown snakes with a mottled dark dorsal surface and a lighter brown ventral one. They are immediately identifiable by a light-colored neck band that crosses from the top of the head to the infralabial region, though it may be interrupted narrowly along the mid-vertebral line and may be doubled along the side, leaving a dark patch on each cheek. The nuchal band is only lightly pigmented. The scales along the posterior edge of the nuchal band may be more densely pigmented than the other dorsal scales on the body. The ventral surface of the body and tail appear uniform beige, with the cloacal region sometimes indicated by a light line.

The pigmentation does not match the scale pattern. The side of the head tends to be dark from the rostral region onto the posterior supralabials, though the individual supralabials and first temporal may be centrally lightened. Similar lightening occurs on the tops of the internasal, prefrontals, and supraoculars and portions of the parietal scales. Some specimens have a very light nuchal band; these show a pair of light spots flanking the midline in the middle of the parietals. Some specimens have a light area with a central dark spot on the posterior supralabials and temporals. This is produced by the confluence of the light areas of the first temporal and fourth and fifth supralabials. On the dorsal surface of the body there are three rows of dark spots. Each spot is approximately the size of (but not coincident with) one dorsal scale. These lie on the level of the vertebral row and the fifth dorsal scale row on each side. Each spot is preceded by a lightly pigmented zone. In some instances similar light regions also occur on dorsal and ventral sides of the spots. Only the middorsal row of spots continues along the tail, the lateral rows fade just posterior to the vent.

Two dark lines or pigment concentrations may occur, respectively between the first and second and second and third dorsals on each side. They become most noticeable about the eighth ventral and continue onto the tail, where they occupy the sutures between the subcaudals and the first dorsal scale row and between the first and second dorsal scale rows. The center of the venter is beige. This color is produced by an even distribution of pigment. Toward the sides of the ventral scales the pattern may fade, producing a mottled effect that differs among specimens.

Locality records.—SRI LANKA: No locality, AMNH 120247 (AL 34), CM 83463 (AL 648c), *BM 74.4.29.1264–1265, 1921.6.15.11, 1931.5.13.71–73, 74.4.29.217, MCZ 15803, *ZSI 7021–7023, 8684–8685, [Colombo Museum, de Silva, 1972.] Near coast, BM 1946.1.12.16–1946.1.12.21, *1946.1.12.22–1946.1.12.26, MCZ 28467 (syntypes of *A. guentheri* Ferguson, 1876; Boulenger, 1890, 1893; Smith, 1943); Ratnapura, 130 m, [Colombo Museum, de Silva, 1972], CM 83464 (CG 092523), FMNH 172302–172306; Yapitikanda, Deniyaya, 500 m, CM 83465 (CG 092512B); Deniyaya, 500 m, CM 83466 (CG 092509B); Kandilpana, Deniyaya, 500 m, USNM 225078–225079 (CG 092514B1–092514B2); Neboda, *BM 97.10.20.12; Yala National Park, AMNH 104446; Rosagalla, MCZ 18053–18054. [Anasigalla Est., Matugama, Kalutara Dist., Colombo Museum, Wall, 1921b, 1923b, 1924; Deraniyagala, 1955; de Silva, 1972]. [Balangoda area, Smith, 1943; Deraniyagala, 1955].

Aspidura trachyrocta Cope

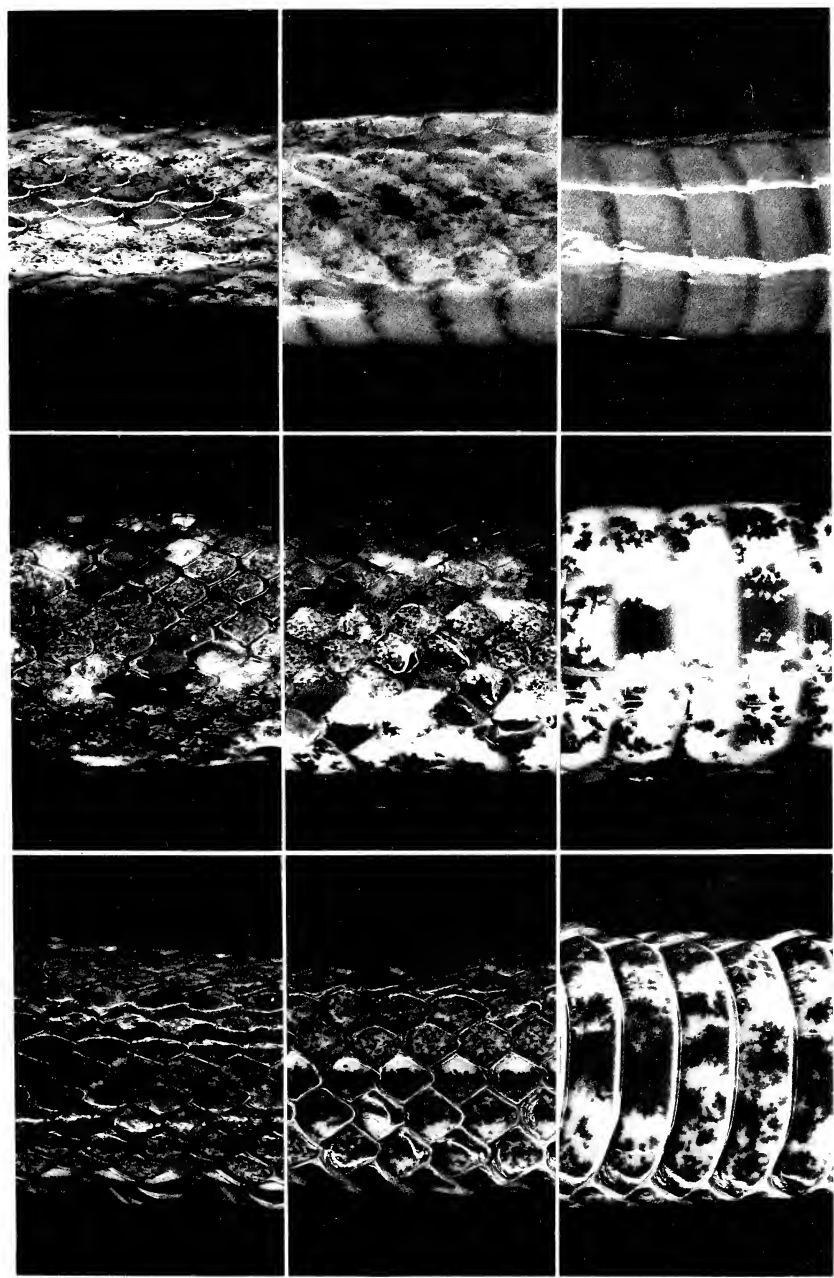
Aspidura trachyrocta Cope, 1860:75–76. Type-locality: "Ceylon." Holotype: ANSP 3308.

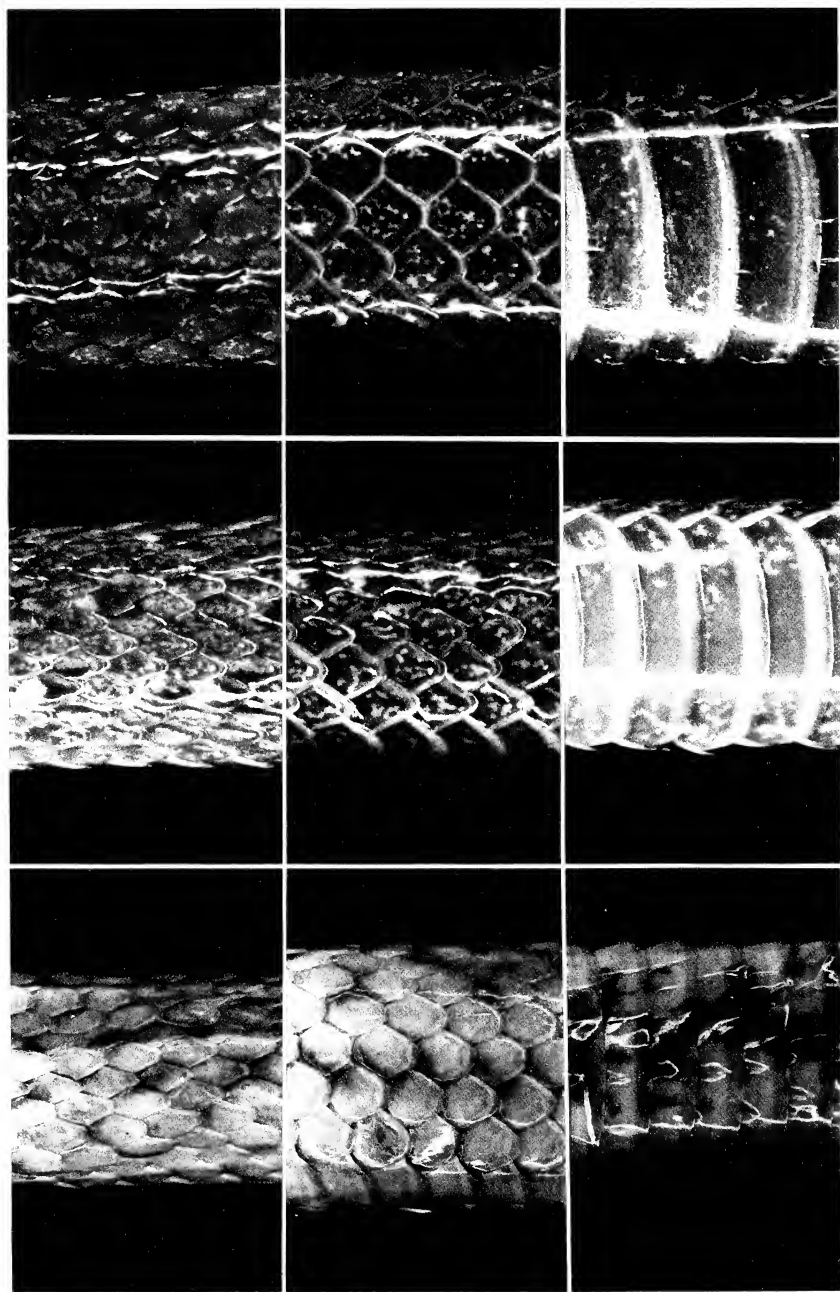
Diagnosis.—This species of *Aspidura* is characterized by a preocular scale that forms part of the anterior border of the orbit; a prefrontal scale that forms the remaining portion of the anterior border of the orbit and contacts supralabials two and three; having the lower postocular longer than the upper; both postoculars in contact with the parietal scale; and the anterior pair of the two pairs of chin shields two to three times the length of the posterior pair.

Fifteen dorsal scale rows are present along the body, except in the region of the head, where two additional rows occur near the dorsal midline. These never persist beyond ventral number 16. The ventral counts range from 128 to 151 (mean = $137.66 \pm .84$, $N = 140$) and subcaudals from 11 to 26 (mean = $18.70 \pm .74$, $N = 139$). The subcaudals are undivided. Snout–vent lengths range from 85 mm to 383 mm, tail lengths from 8 mm to 40 mm, midbody diameters from 2.5

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Fig. 8—Dorsal (left), lateral (middle), and ventral (right) views at midbody of *Aspidura brachyorrhos* (top), *A. copei* (middle), and *A. deraniyagalae* (bottom). Same specimens as Figs. 4 and 5.





mm to 13.9 mm (Table 2). Females tend to have more ventrals, and shorter tails than males, but males and females do not differ in total length. Fig. 2 compares the major counts, Fig. 3 the body proportions, and Figs. 7, 9, and 12 illustrate specimens.

Color pattern (preserved specimens).—These are stout brown snakes with a spectacular diversity of dorsal and ventral coloration. They range from an extremely dark blackish brown dorsal surface, sometimes relieved by traces of lighter interscalar skin, to a light brown dorsal color with indications of lateral stripes and two or usually three rows of dark dorsal spots. In the dark specimens the head is totally dark, in light individuals there is indication of a light, dark-bordered lateral stripe running posteriorly from the snout, often interrupted above the eye, and continuing across the lateral edges of the parietals onto the temporals. The light stripe on the head is faintly noticeable even in very dark specimens. Posterior to the orbit it reaches from the anteriolateral portion of the parietals backward to the dorsal half of the temporals and onto the two or three dorsals flanking the first and second vertebrae. The second vertebral is sometimes light providing a confluence between the light stripes of the two sides.

A dark stripe starting near the internasal, spreads posteriorly over the ventral edges of the prefrontals to include the eye, passes over the temporals and the first two to four dorsal scales posterior to the temporals and then bends first ventrally and then posteriorly sometimes forming a dark lateral stripe on dorsal scale rows two and three on each side of the body. The stripe may become continuous with a lateral stripe present between dorsal scale rows two and three along the body. A dark region extends over the azygous frontal and the middle of the two parietals, and continues posteriorly along the anterior portion of the vertebral scale row. The frontal and the dorsal halves of the parietals tend to be well pigmented. The supraocular scales may be lightened. The supralabials are light colored except for the sutures. The zone posterior to the angle of the mouth is also lightly pigmented.

Often the light beige colored dorsal surface is marked by a row of vertebral spots. Each of these spots is approximately as large as a single dorsal scale and successive spots in a series are separated by two to four lightly pigmented dorsals. The spots are flanked on each side by a row of staggered spots also about as large as a single dorsal scale. The array of these dorsal spots is very irregular. Sometimes the

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Fig. 9.—Dorsal (left), lateral (middle), and ventral (right) views at midbody of *Aspidura drummondhayi* (top), *A. guentheri* (middle), and *A. trachyprocta* (bottom). Same specimens as Figs. 5 and 6.

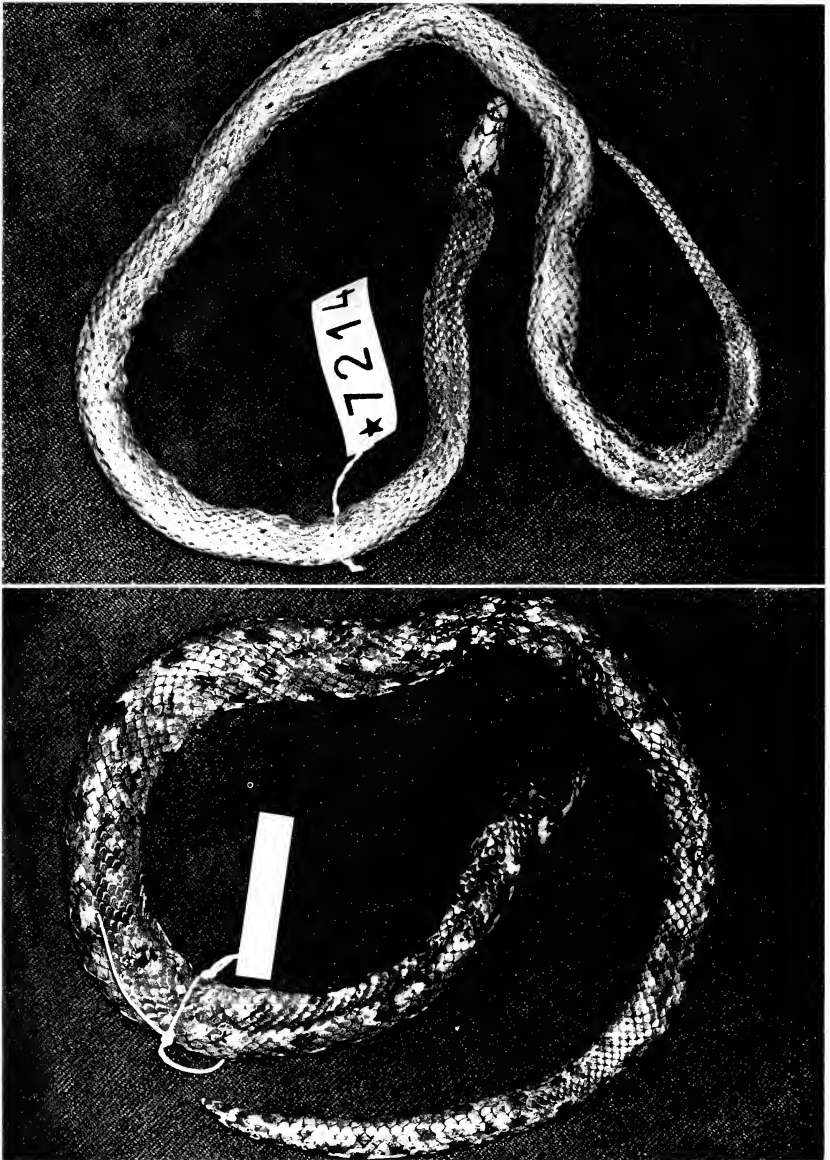


Fig. 10.—Dorsal views of whole specimens of (top) *Aspidura brachyorrhos* (MNHP 7214) and (bottom) *A. copei* (BM 1946.1.12.9).

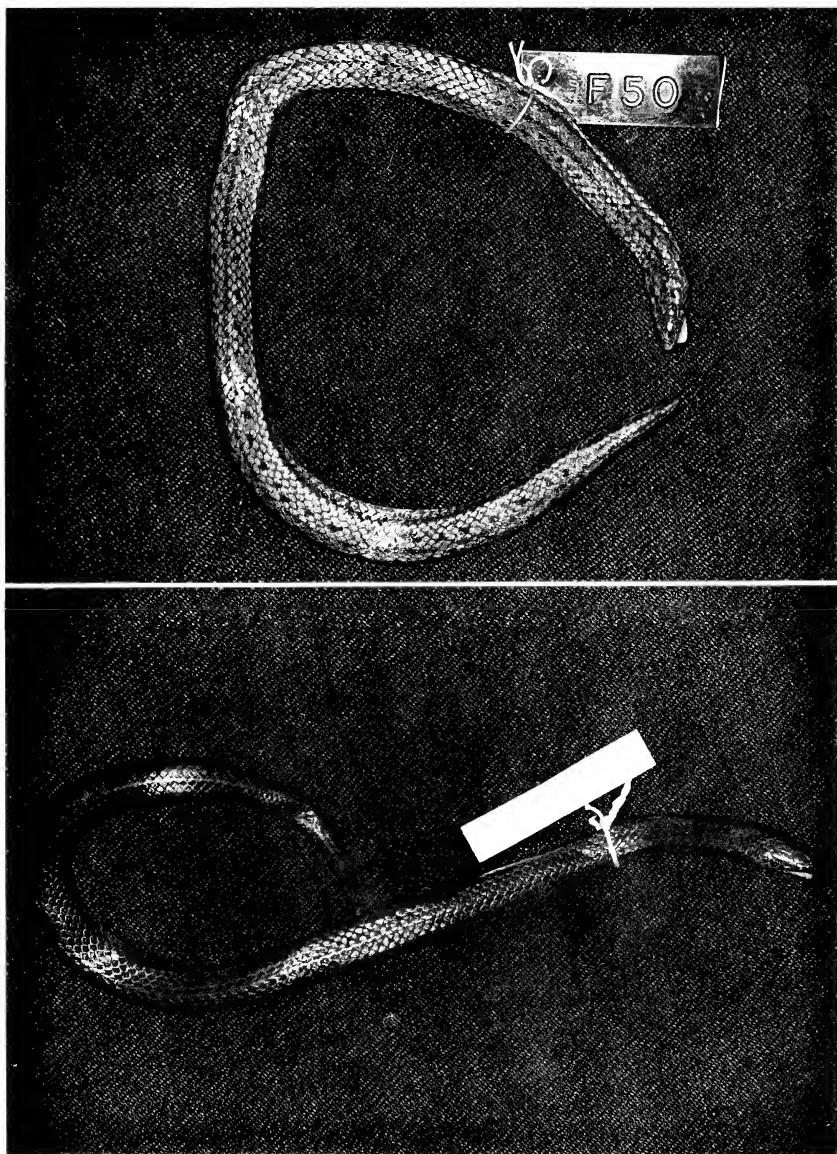


Fig. 11.—Dorsal views of whole specimens of (top) *Aspidura deraniyagalae* (paratype, CM 83456) and (bottom) *A. drummondhayi* (BM 1946.1.12.45).



Fig. 12.—Dorsal views of whole specimens of (top) *Aspidura guentheri* (BM 1946.1.12.19) and (bottom) *A. trachyprocta* (AMNH 120249).

spots in the midline drop out for short intervals, or are absent along the entire body. The various dorsal blotches approach each other and tend to coalesce near the level of the cloaca and form a dark vertebral stripe that runs along the tail to its tip.

The zone between the second and third dorsal scale rows on each side tends to be darkened, giving the impression of a more or less continuous dark stripe that extends either along the entire body, or only on the posterior two thirds of the body, becoming gradually wider and continuing onto the tail. Very dark specimens have an unmarked dorsal surface anterior to the level of the fifteenth ventral preceeding the vent. More posteriorly they show a series of light colored areas distributed along either the dorsal portion of the third dorsal scale row or the fourth dorsal scale row on each side; these give the impression of a poorly expressed, light lateral stripe that extends onto the tail in lighter colored specimens. This light stripe may run the entire length of the body in those animals having a complete dark stripe between scale rows two and three.

Only a few generalizations can be made about the pattern of ventral pigmentation. The ventral surface may be heavily blotched with black, which often becomes solid in the precloacal region and on the tail. The opposite end of the spectrum is a completely light colored ventral surface, lacking more than incidental blotching except on the midline of the tail. In most animals the pigmentation tends to be darker posteriorly. Usually the ventral surface shows a striking contrast between light and dark colors; however, a few specimens show dispersed pigmentation in the light colored regions. A dark midventral line is often present. This is usually formed by dark medial blotches though these may not occur on every scale. In some specimens these blotches form an irregular pattern. In other specimens the midline is light and the dark dorsal color extends variably onto the sides of the ventrals.

Living specimens vary between light reddish brown and blackish-brown dorsally with the ventral surface yellowish (sometimes with a reddish tint) and the ventral blotches brown to black.

Locality records.—SRI LANKA: No locality (in mountains), CM 83486 (AL 638b), AMNH 24671, ANSP 3308 (holotype of *A. trachyprocta* Cope, 1860), *BM 60.3.19.1266, 80.2.2.120, FMNH 10901, 27264, 124118–124119, *KU 68900, MCZ 3174, 9304, [Vienna-Novara Museum, Jan, 1862, 1863; Jan and Sordelli, 1865, (13), pl. 2, 1], USNM 19214, 56150 (Taylor, 1950), *ZSI 4424, 7025, (Günther, 1864; Boulenger, 1890, 1893, 1896; Theobald, 1876); Gammaduwa, 750 m, CM 83468 (F 375); Monaragala, FMNH 142404; Labukelle, 1733 m, CM 83536–83539 (AL 546a–546d); USNM 225083–225090 (AL 546e–546i); Harasbedda, 1355 m, CM 83469 (AL 574); Eskdale, 1716 m, CM 83470–83471 (AL 217a–217b), AMNH 120248 (AL 217c), CM 83534 (AL 218, broken); Medamaha Nuwara, 3500–4000 ft, *BM 1969.2735–2742; Pundaluoya, 4000 ft, *BM 1905.3.25.92–1905.3.25.94; Langton Estate, (nr. Talawakele), 1230 m, CM 83472–83475 (F 153–156); Talawakele, Diyagama West Estate, 4500 ft, CM 83535 (AL 228, broken), FMNH

121474–121479; Nuwara Eliya, 2100 m, CM 83476–83477 (AL 461a–461b), AMNH 94447, *KU 24139 (Taylor, 1950), *ZMB 3035, [Geneva, Jan. 1863; Jan and Sordelli, 1865, (13), pl. 2, 3; Deraniyagala, 1955]; Nanu Oya, (4000–5000 ft) FMNH 131365–131370; Sita Eliya, 1740 m, CM 83478–83482 (F 82–89); Maha-Eliya, 5000–6000 ft, FMNH 121947–121948; Ambawela, 1790 m, CM 83487–83498 (F 90–104), CM 83483–83485, 83500–83507 (F 107–117); Pattipola, 1890 m, AMNH 85082, CM 83499 (F 105), *NMSL C1A, *ZSI 17032, 17555 (6200 ft); Garden above Hakgala, F 81 (eggs); Horton plains, AMNH 85081, *NMSL C1/A–F (Wall, 1905), *ZSI 17553–17554; Bopatalawa, Horton Plains, *BM 1972.2175–1972.2176; Ohiya, *NMSL E-1; Pindarawatta (at Namunukula), 1500 m, CM 83508 (AL 35a), AMNH 120249 (AL 35c), CM 83509–83510 (AL 35d–35e), CM 83511–83518 (AL 72a–72h), CM 83519 (AL 75c), CM 83520 (AL 88), USNM 225080–225082 (AL 157a–157c), CM 83521–83522 (AL 167e–167f), CM 83523–83524 (AL 185a–185b), CM 83525 (AL 190), CM 83533 (AL 219); Kanawarella group, (above Namunukula), 1520 m, CM 83526–83528 (F 42–44), CM 83529–83532 (F 46–49), AMNH 120250–120251 (F 51–52); Namunukula, 4000 ft (in trench) FMNH 120908–120910, 120912; Kurnbakkann (?), MCZ 34890–34908. [Kandy, Radella, Ramboda and Diyatalava, Deraniyagala, 1955]. [Uva Patnas (district), Wall, 1921a, Deraniyagala, 1955; considered error, Wall, 1923c]. [Kambaddy, ZSI 7015 (not located), Sclater, 1891]. [Maldiv Islands: Malé Atoll, Laidlaw, 1902. Phillips, 1958, makes reference to this unlikely report, but notes under his entry for *Lycodon aulicus* “said to be the only snake known in Malé.” However, Laidlaw, 1902, did note that “the close connection with Ceylon is probably a growth of quite recent date. The principal trade relations . . .,” a phrasing that suggests his view that some of the fauna might have been introduced by man.] As *Aspidura trachyprocta* is a montane form and as montane *Aspidura* are quite sensitive to elevated temperatures and die within days when brought down to sea level (Gans unpublished), and as the earlier report of *Aspidura trachyprocta* from the Malé atoll is undocumented by any specimen, it is here considered to be in error.

Species incertae sedis

Haly's (1886, 1889) comments on various species lack sufficient information to evaluate his identifications. Nicholson (1893) listed *A. brachyorrhos*, *A. copei*, and *A. trachyprocta* without localities and with misleading characterizations. Fletcher (1908) cites an *A. trachyprocta* from Bandarawela that has a preocular on one side only. Pearlless (1909) cites *A. brachyorrhos* from Badulla without further reference. Sarasin (1910) lists the species in a table.

de Silva (1972) lists as *A. trachyprocta* a number of Colombo Museum specimens from Ratnapura, Haputale, Kotmale, Pattipola, Nanu Oya, Dickoya, Hakgala, and Horton Plains. However, his definition of the species mentions that the upper postocular is larger than the lower and notes that only the upper postocular contacts the parietal. These characters never occur in specimens here assigned to *A. trachyprocta*, but are characteristic of the form here called *A. guentheri*.

The data for some of the specimens collected by the Brothers Sarasin appear to have become mixed. Thus, Müller notes two (1885), 11 (1887), and two (1890) specimens of *A. trachyprocta* from Nuwara Eliya and five *A. brachyorrhos* from “Peradenia, Nuwera Ellia” (Mül-

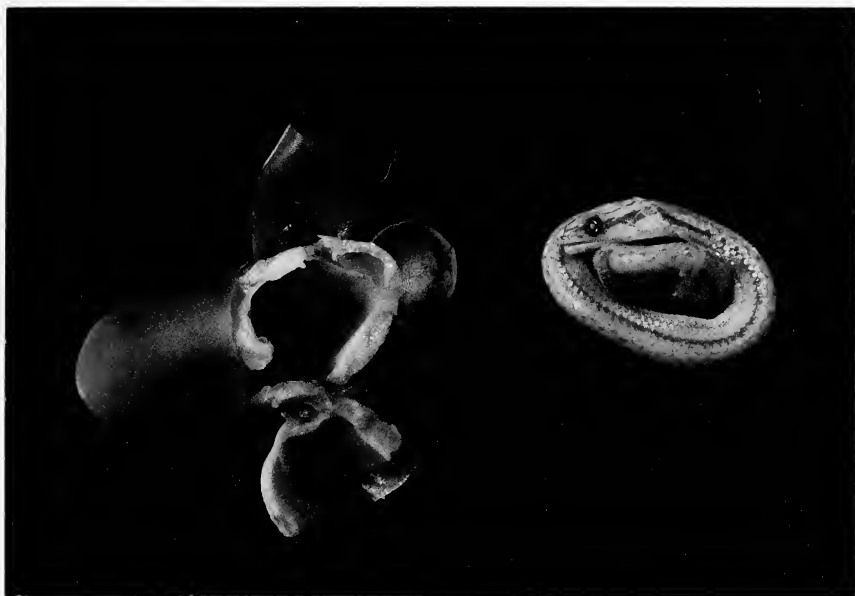


Fig. 13.—Egg shell and embryo (one of five) of *Aspidura trachyprocta* taken near Hakgala (F 81).

ler, 1887); the latter clearly representing a mixture of two disparate sites.

BIOLOGICAL OBSERVATIONS

Aspidura brachyorrhos.—Some specimens (CM 83448, AL 103a; AMNH 120244, AL 1036) were found in tea plantations among ground cover. FMNH 120911 is labelled “‘4000’ in trench” a label that also applies to an *A. trachyprocta*. BM 1968.872 is labelled “‘3500’, dug up in loose soil on steep river bank.” The species deposits two to five eggs measuring 28 by 8 mm (Wall, 1921a; Smith, 1943; Deraniyagala, 1955). In the present sample, egg numbers were five in CM 83448 (AL 103a) and CM 83446 (AL 648a), and six in CM 83451 (AL 548a).

Aspidura copei.—A female taken at Avissawella in January 1906 contained 21 eggs, measuring $3/4$ " by $1/2$ " (not 20 by 103 mm, as in Deraniyagala, 1955; Willey, 1906, see above).

Aspidura deraniyagalae.—Specimens were taken in humus (CM 83455, F 45) or mulch (AMNH 120246, F 64; CM 83457, F 65) piles in irrigated agricultural land amid tea bushes. In the present sample egg

numbers were two in CM 83461 (AL 167c) and USNM 225091 (AL 75a) and four in CM 83458 (AL 35b).

Aspidura drummondhayi.—The holotype was noted to be “viviparous,” and was taken from drains in the same field as *Aspidura copei* (Boulenger, 1904). Specimen CM 83467 (CG 092519B) contained four eggs.

Aspidura guentheri.—Wall (1921b) mentions two eggs, but later (1923b, 1924) noted that almost all specimens of a much larger series each contained only a single egg. In the present sample, egg numbers were two in CM 83466 (CG 092509B) and USNM 225078 (CG 092514B1) and three in USNM 225079 (CG 092514B2). Wall (1921b, 1923b, 1924) reported the presence of earthworms in the stomachs of some specimens.

Aspidura trachyprocta.—A series of specimens F 50, CM 83526–83532 (F 42–49), AMNH 120250–120251 (F 51–52) were collected above Namunukula in the same field and humus piles as *Aspidura deraniyagalae* and *Rhinophis drummondhayi*. Prefers leaf mold and rotten timber. Oviparous, 4 to 12 eggs, 25 by 16 mm. The eggs of the two ovaries mature sequentially “probably due to two separate copulations” (Deraniyagala, 1955). In the present series, egg count was six in CM 83522 (AL 167f). A clutch of five, near-term eggs was dug up from a depth of 15 cm in a moist, grassy open area near Hakgala (Fig. 13). *A. trachyprocta* apparently feed on earthworms (Wall, 1921a). Wall (1921a) found a specimen of *A. trachyprocta* in the stomach of another snake, “*Ancistrodon hypnale*.” Parasitized by nematode *Kali-cephalus brachycephalus* (Crusz and Sanmugasunderam, 1974).

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HERPETOLOGICAL TYPE-SPECIMENS IN CARNEGIE MUSEUM OF NATURAL HISTORY: SUPPLEMENT

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INTRODUCTION

A list of herpetological type-specimens in Carnegie Museum of Natural History was published in 1966 (McCoy and Richmond, 1966, *Annals of Carnegie Museum* 38:233-264). In that list 916 type-specimens, representing 195 nominal taxa of amphibians and reptiles, were cited. The type-specimens included in the 1966 list were accumulated through the first 40 years of the Section's history.

In the ensuing 16 years both the number of type-specimens and the number of taxa represented by type-material in the collection have approximately doubled, to 1827 and 386 respectively. The greatest part of this increment has resulted from research by Section staff, and from deposition of type-specimens by Research Associates of the Section, notably Carl Cans, Coleman J. Goin, and Albert Schwartz. Other type-material has been received as gifts or in exchange from many sources. A few type-specimens that were overlooked in the earlier compilation are listed here, as are a few that have been re-catalogued to eliminate duplication of numbers.

The impetus for compilation of this supplementary list of type-specimens was completion of a computerized collection data management

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system, which has greatly facilitated identification and listing of the type-material. In this list, unlike the 1966 list, we present the names of taxa only as originally proposed. As most of the taxa included are recently described, the elimination of cross-references for forms that have been relegated to synonymy or placed in different generic combinations should present no major problems. For each taxon listed we provide date of publication and a bibliographic citation to the original description. Following the bibliographic citation is a list of all type-specimens in Carnegie Museum of Natural History (holotype, if present, followed by paratypes), by catalogue number (CM) and general locality. This list records all type-specimens, except those cited in the 1966 list, catalogued to 1 July 1982.

ORDER CAUDATA

Ensatina eschscholtzi picta Wood, 1940, Univ. California Publ. Zool., 42:425.

CM 17287 (paratype)—California.

Plethodon dixi Pope and Fowler, 1949, Nat. Hist. Misc., 47:1.

CM 26263 (27 paratypes)—Virginia.

Plethodon hoffmani Highton, 1971, Virginia Polytech. Inst., Res. Div. Monogr., 4:151.

CM 34992 (paratype)—Virginia.

Plethodon nettingi Green (see McCoy and Richmond, 1966:241).

CM 11809 (paratype)—West Virginia.

Plethodon richmondi shenandoah Highton and Worthington, 1967, Copeia, 1967:619.

CM 40532–40533 (paratypes)—Virginia.

Plethodon shermani rabunensis Pope and Hairston, 1948, Copeia, 1948:106.

CM 17781 (17 paratypes), 17790 (25 paratypes), 17812 (41 paratypes)—Georgia.

ORDER SALIENTIA

Afrixalus orophilus Laurent, 1947, Bull. Mus. Roy. Hist. Nat. Belgique, 23:1.

CM 63052–63053 (paratypes)—Zaire.

Bufo fluviaticus Schwartz, 1972, J. Herpetol., 6:226.

CM 54074 (holotype), 54064–54073 (paratypes)—Republica Dominicana.

Bufo funereus upembae Schmidt and Inger, 1959, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 56:17.

CM 57195, 63361 (paratypes)—Zaire.

Bufo guntheri fractus Schwartz, 1972, J. Herpetol., 6:218.

CM 54055–54063 (paratypes)—Republica Dominicana.

- Bufo melanopleura* Schmidt and Inger, 1959, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 56:23.
CM 57194, 63432 (paratypes)—Zaire.
- Callixalus pictus* Laurent, 1950, Rev. Zool. Bot. Afr., 44:6.
CM 46062–46064 (paratypes)—Zaire.
- Chrysobatrachus cupreonitens* Laurent, 1951, Rev. Zool. Bot. Afr., 44:378.
CM 46065–46066 (paratypes)—Zaire.
- Eleutherodactylus alcoae* Schwartz, 1971, Ann. Carnegie Mus., 43:26.
CM 45889 (holotype)—Republica Dominicana.
- Eleutherodactylus apostates* Schwartz, 1973, J. Herpetol., 7:262.
CM 54093 (holotype)—Haiti.
- Eleutherodactylus chlorophenax* Schwartz, 1976, Herpetologica, 32:168.
CM 56833 (holotype)—Haiti.
- Eleutherodactylus cundalli glaucoreius* Schwartz and Fowler, 1973, Stud. Fauna Caraçao Carib. Islands, 43:73.
CM 52801–52832 (paratypes)—Jamaica.
- Eleutherodactylus eunaster* Schwartz, 1973, J. Herpetol., 7:250.
CM 54094 (paratype)—Haiti.
- Eleutherodactylus fowleri* Schwartz, 1973, J. Herpetol., 7:255.
CM 54095–54096 (paratypes)—Republica Dominicana.
- Eleutherodactylus glaphycompus* Schwartz, 1973, J. Herpetol., 7:253.
CM 54092 (holotype), 54097–54101 (paratypes)—Haiti.
- Eleutherodactylus gossei oligaulax* Schwartz and Fowler, 1973, Stud. Fauna Caraçao Carib. Islands, 43:95.
CM 52833–52856 (paratypes)—Jamaica.
- Eleutherodactylus lamprotes* Schwartz, 1973, J. Herpetol., 7:253.
CM 54091 (holotype)—Haiti.
- Eleutherodactylus lucioi* Schwartz, 1980, Ann. Carnegie Mus., 49:105.
CM 60537 (holotype)—Haiti.
- Eleutherodactylus octavioi* Bokermann, 1965, Copeia, 1965:440.
CM 39907 (paratype)—Brazil.
- Eleutherodactylus pantoni amiantus* Schwartz and Fowler, 1973, Stud. Fauna Curaçao Carib. Islands, 43:109.
CM 52299, 52863–52875, 52882–52900 (paratypes)—Jamaica.
- Eleutherodactylus pantoni pentasyringos* Schwartz and Fowler, 1973, Stud. Fauna Curaçao Carib. Islands, 43:114.
CM 52297–52298, 52857–52862, 52876–52881 (paratypes)—Jamaica.
- Eleutherodactylus pictissimus apanteatus* Schwartz, 1965, Stud. Fauna Curaçao Carib. Islands, 22:102.
CM 38973–38978 (paratypes)—Republica Dominicana.
- Eleutherodactylus pinchoni* Schwartz, 1967, Stud. Fauna Curaçao Carib. Islands, 24:45.
CM 40584–40585 (paratypes)—Guadeloupe.

- Eleutherodactylus rhodesi* Schwartz, 1980, Ann. Carnegie Mus., 49:108.
CM 60538 (holotype)—Haiti.
- Eleutherodactylus savagei* Pyburn and Lynch, 1981, Proc. Biol. Soc. Washington, 94:404.
CM 76154–76162 (paratypes)—Colombia.
- Eleutherodactylus sciagraphus* Schwartz, 1973, J. Herpetol., 7:259.
CM 54102–54103 (paratypes)—Haiti.
- Eleutherodactylus supernatis* Lynch, 1979, J. Herpetol., 13:415.
CM 75042 (paratype)—Ecuador.
- Eleutherodactylus urichi euphronides* Schwartz, 1967, Stud. Fauna Curaçao Carib. Islands, 24:6.
CM 40579–40583 (paratypes)—Grenada.
- Eleutherodactylus warreni* Schwartz, 1976, Bull. Florida State Mus., 21:26.
CM 54138 (holotype), 54139 (paratype)—Haiti.
- Eleutherodactylus weinlandi paralius* Schwartz, 1976, Bull. Florida State Mus., 21:16.
CM 54132–54137 (paratypes)—Republica Dominicana.
- Eleutherodactylus wetmorei ceraemerus* Schwartz, 1968, Breviora, 290:5.
CM 37786, 38550–38555 (paratypes)—Haiti.
- Eleutherodactylus wetmorei sommeri* Schwartz, 1977, Herpetologica, 33:68.
CM 56837 (holotype), 56838–56850 (paratypes)—Haiti.
- Elosia ornata* Bokermann, 1967, Neotropica, 13:135.
CM 45148 (paratype)—Brazil.
- Gastrotheca aureomaculata* Cochran and Goin, 1970, U.S. Natl. Mus. Bull., 288:177.
CM 50397 (paratype)—Colombia.
- Gastrotheca mertensi* Cochran and Goin, 1970, U.S. Natl. Mus. Bull., 288:181.
CM 50395–50396 (paratypes)—Colombia.
- Hyla blairi* Fouquette and Pyburn, 1972, Herpetologica, 28:176.
CM 54356 (paratype)—Colombia.
- Hyla boesemani* Goin, 1966, Zoologische Mededelingen, 41:229.
CM 41595, 50471–50473, 50492 (paratypes)—Suriname.
- Hyla cabrerai* Cochran and Goin, 1970, U.S. Natl. Mus. Bull., 288:215.
CM 50406 (paratype)—Colombia.
- Hyla fuentei* Goin and Goin, 1968, Copeia, 1968:581.
CM 44218 (holotype)—Suriname.
- Hyla guibei* Cochran and Goin, 1970, U.S. Natl. Mus. Bull., 288:233.
CM 50398, 50403 (paratypes)—Colombia.
- Hyla mathiassoni* Cochran and Goin, 1970, U.S. Natl. Mus. Bull., 288:286.

- CM 50428–50430 (paratypes)—Colombia.
- Hyla riveroi* Cochran and Goin, 1970, U.S. Natl. Mus. Bull., 288:284.
CM 37433 (holotype), 36085 (11 paratypes), 50205 (paratype)—Colombia.
- Hyperolius kibarae* Laurent, 1957, Expl. Parc Natl. Upemba Miss. G. F. de Witte, 42:8.
CM 63072–63073 (paratypes)—Zaire.
- Hyperolius marmoratus epheboides* Laurent, 1957, Expl. Parc. Natl. Upemba Miss. G. F. de Witte, 42:21.
CM 63081–63082 (paratypes)—Zaire.
- Hyperolius platyceps major* Laurent, 1957, Expl. Parc Natl. Upemba Miss. G. F. de Witte, 42:6.
CM 63089 (paratype)—Zaire.
- Kassina senegalensis ruandae* Laurent, 1972, Expl. Parc Nat. Albert, 22:54.
CM 46060–46061 (paratypes)—Burundi.
- Megalophrys ligayae* Taylor (see McCoy and Richmond, 1966:247).
CM 84521 (holotype, formerly 3304), 84522 (paratype, formerly 3305)—Philippines.
- Megalophrys stejnegeri* Taylor (see McCoy and Richmond, 1966:247).
CM 84517–84520 (paratypes, formerly 3300–3303)—Philippines.
- Phrynobatrachus anotis* Schmidt and Inger, 1959, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 56:139.
CM 62677–62678 (paratypes)—Zaire.
- Phrynobatrachus cryptotis* Schmidt and Inger, 1959, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 56:143.
CM 62680–62681 (paratypes)—Zaire.
- Physalaemus aguirrei* Bokermann, 1966, Physis, 26:194.
CM 45157 (paratype)—Brazil.
- Physalaemus centralis* Bokermann, 1962, Rev. Bras. Biol., 22:216.
CM 50217 (paratype)—Brazil.
- Physalaemus cicada* Bokermann, 1966, Rev. Bras. Biol., 26:257.
CM 45150 (paratype)—Brazil.
- Physalaemus jordanensis* Bokermann, 1967, Rev. Bras. Biol., 27:135.
CM 45160 (paratype)—Brazil.
- Physalaemus obtectus* Bokermann, 1966, Physis, 26:197.
CM 45158–45159 (paratypes)—Brazil.
- Ptychadena gansi* Laurent, 1965, Ann. Mus. Roy. Afrique Cent., ser. 8°, 134:18.
CM 38696 (paratype)—Somalia.
- Rana desaegeri* Laurent, 1972, Expl. Parc Nat. Virunga, 2nd ser., 22:91.
CM 46069–46070 (paratypes)—Zaire.
- Rana magnaocularis* Frost and Bagnara, 1976, Copeia, 1976:332.
CM 67208 (paratype)—Mexico.

- Rana obscura* Schmidt and Inger, 1959, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 56:85.
CM 62699–62700 (paratypes)—Zaire.
- Rana palustris mansuetii* Hardy, 1964, Chesapeake Sci., 5:91.
CM 19486 (paratype)—North Carolina.
- Rana ruwenzorica* Laurent, 1972, Expl. Parc Nat. Virunga, 2nd ser., 22: 93.
CM 46067–46068 (paratypes)—Zaire.
- Rana upembae* Schmidt and Inger, 1959, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 56:111.
CM 62705–62706 (paratypes)—Zaire.
- Rana philippinensis* Taylor (see McCoy and Richmond, 1966:249).
CM 84523 (holotype, formerly 3306)—Philippines.
- Sphaenorhynchus bromelicola* Bokermann, 1966, Rev. Bras. Biol., 26: 18.
CM 46051 (paratype)—Brazil.
- Synapturanus salseri* Pyburn, 1975, Herpetologica, 31:440.
CM 58829 (paratype)—Colombia.
- Trachycephalus atlas* Bokermann, 1966, Neotropica, 12:120.
CM 46052–46053 (paratypes)—Brazil.

ORDER TESTUDINES

- Pelusios williamsi lutescens* Laurent, 1965, Ann. Mus. Roy. Afrique Cent., ser. 8°, 135:16.
CM 62248 (paratype)—Zaire.

ORDER SQUAMATA

Suborder Amphisbaenia

- Amphisbaena minuta* Hulse and McCoy, 1979, Ann. Carnegie Mus., 48: 2.
CM 65531 (holotype), 65532–65533 (paratypes)—Argentina.
- Amphisbaena xera* Thomas, 1966, Breviora, 249:7.
CM 40577–40578 (paratypes)—Puerto Rico.
- Bipes canaliculatus multiannulatus* Alvarez, 1964, Ann. Esc. Nac. Cienc. Biol. Mexico, 8:147.
CM 45934–45936 (paratypes)—Mexico.
- Monopeltis capensis rhodesianus* Broadley, Gans and Visser, 1976, Bull. Amer. Mus. Nat. Hist., 157:394.
CM 61601–61602 (paratypes)—Zimbabwe.

Suborder Sauria

- Acanthodactylus busacki* Salvador, 1982 Bonner Zool. Monogr., 16:88.
CM 55212–55213 (paratypes)—Morocco.
- Afroedura transvaalica loveridgei* Broadley, 1963, Ann. Mag. Nat. Hist., ser. 13, 6:286.

- CM 47582, 61593–61594 (paratypes)—Mozambique.
- Ameiva auberi atrothorax* Schwartz, 1970, Ann. Carnegie Mus., 41:79.
CM 40641–40642 (paratypes)—Cuba.
- Ameiva auberi bilateralis* McCoy, 1970, Ann. Carnegie Mus., 41:142.
CM 40985 (holotype), 40955–40959, 40984, 40988–40995 (paratypes)—Bahamas.
- Ameiva auberi felis* McCoy, 1970, Ann. Carnegie Mus., 41:128.
CM 20440 (holotype)—Bahamas.
- Ameiva auberi focalis* McCoy, 1970, Ann. Carnegie Mus., 41:137.
CM 41147 (holotype), 41139–41146 (paratypes)—Bahamas.
- Ameiva auberi garrioi* Schwartz, 1970, Ann. Carnegie Mus., 41:77.
CM 40638–40640 (paratypes)—Cuba.
- Ameiva auberi kingi* McCoy, 1970, Ann. Carnegie Mus., 41:130.
CM 40915 (holotype), 40916–40920 (paratypes)—Bahamas.
- Ameiva auberi marcida* Schwartz, 1970, Ann. Carnegie Mus., 41:105.
CM 40647–40648 (paratypes)—Cuba.
- Ameiva auberi multilineata* McCoy, 1970, Ann. Carnegie Mus., 41:132.
CM 41196 (holotype), 41160, 41195, 41197–41199 (paratypes)—Bahamas.
- Ameiva auberi obsoleta* McCoy, 1970, Ann. Carnegie Mus., 41:139.
CM 43976 (holotype)—Bahamas.
- Ameiva auberi peradusta* Schwartz, 1970, Ann. Carnegie Mus., 41:83.
CM 40643–40646 (paratypes)—Cuba.
- Ameiva auberi richmondi* McCoy, 1970, Ann. Carnegie Mus., 41:134.
CM 34140 (holotype), 32589, 34112–34114, 34130, 34139, 34141–34145 (paratypes)—Bahamas.
- Ameiva auberi zugi* Schwartz, 1970, Ann. Carnegie Mus., 41:107.
CM 40649–40650 (paratypes)—Cuba.
- Ameiva chrysolema evulsa* Schwartz, 1973, Herpetologica, 29:101.
CM 54075–54090 (paratypes)—Haiti.
- Ameiva taeniura aequorea* Schwartz, 1967, Bull. Mus. Comp. Zool. 135:353.
CM 40559–40561 (paratypes)—Haiti.
- Ameiva taeniura regnatrix* Schwartz, 1967, Bull. Mus. Comp. Zool., 135:351.
CM 40555–40558 (paratypes)—Haiti.
- Ameiva taeniura tofacea* Schwartz, 1967, Bull. Mus. Comp. Zool., 135:362.
CM 40562–40563 (paratypes)—Republica Dominicana.
- Ameiva thoracica* Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 14:64.
CM 43723–43724 (paratypes)—Bahamas.
- Anolis bahorucoensis southerlandi* Schwartz, 1978, J. Herpetol., 12:357.
CM 60514 (holotype)—Republica Dominicana.

Anolis baleatus caeruleolatus Schwartz, 1974, Bull. Mus. Comp. Zool., 146:126.

CM 54119–54126 (paratypes)—Republica Dominicana.

Anolis baleatus litorisilva Schwartz, 1974, Bull. Mus. Comp. Zool., 146:133.

CM 54113–54114 (paratypes)—Republica Dominicana.

Anolis baleatus multistruppis Schwartz, 1974, Bull. Mus. Comp. Zool., 146:121.

CM 54107–54112 (paratypes)—Republica Dominicana.

Anolis baleatus samanae Schwartz, 1974, Bull. Mus. Comp. Zool., 146:130.

CM 54105 (holotype), 54127–54130 (paratypes)—Republica Dominicana.

Anolis baleatus scelestus Schwartz, 1974, Bull. Mus. Comp. Zool., 146:135.

CM 54106 (holotype), 54115–54118 (paratypes)—Republica Dominicana.

Anolis baleatus sublimis Schwartz, 1974, Bull. Mus. Comp. Zool., 146:124.

CM 54104 (holotype)—Republica Dominicana.

Anolis coelestinus pecuarius Schwartz, 1969, Caribbean J. Sci., 9:34.

CM 45852–45866 (paratypes)—Haiti.

Anolis distichus aurifer Schwartz, 1968, Bull. Mus. Comp. Zool. 137:291.

CM 40613–40616 (paratypes)—Haiti.

Anolis distichus dapsilis Schwartz, 1968, Bull. Mus. Comp. Zool., 137:270.

CM 40623–40629 (paratypes)—Bahamas.

Anolis distichus favillarum Schwartz, 1968, Bull. Mus. Comp. Zool., 137:289.

CM 40609–40612 (paratypes)—Republica Dominicana.

Anolis distichus ravitergum Schwartz, 1968, Bull. Mus. Comp. Zool., 137:287.

CM 40604–40608 (paratypes)—Republica Dominicana.

Anolis distichus suppar Schwartz, 1968, Bull. Mus. Comp. Zool., 137:295.

CM 37811 (11 paratypes)—Haiti.

Anolis distichus vinosus Schwartz, 1968, Bull. Mus. Comp. Zool., 137:293.

CM 40617–40622 (paratypes)—Haiti.

Anolis eugenegrahami Schwartz, 1978, Ann. Carnegie Mus., 47:266.

CM 60515 (holotype), 60516–60518 (paratypes)—Haiti.

Anolis fowleri Schwartz, 1973, Ann. Carnegie Mus., 44:186.

CM 54131 (holotype)—Republica Dominicana.

- Anolis occultus* Williams and Rivero, 1965, Breviora, 231:4.
CM 40691–40692 (paratypes)—Puerto Rico.
- Anolis sheplani* Schwartz, 1974, Breviora, 423:4.
CM 52300, 54140–54141 (paratypes)—Republica Dominicana.
- Cnemidophorus tigris punctatus* Walker and Maslin, 1965, Univ. Colorado Stud., Ser. Biol., 20:3.
CM 40216, 40219, 40310–40316, 40318, 40320–40327, 40329–40332, 40334, 40336, 40339–40352, 40354–40356, 40426–40429 (paratypes)—Mexico.
- Diploglossus agasepsoides* Thomas, 1971, Occas. Papers Mus. Zool. Louisiana State Univ., 40:2.
CM 45893–45894 (paratypes)—Republica Dominicana.
- Diploglossus costatus emys* Schwartz, 1971, J. Herpetol., 5:163.
CM 52286, 52293–52296 (paratypes)—Haiti.
- Diploglossus costatus saonae* Schwartz, 1971, J. Herpetol., 5:161.
CM 52285 (holotype)—Republica Dominicana.
- Eremias savagei* Laurent and Gans, 1965, Ann. Mus. Roy. Afrique Cent., ser. 8°, 134:39.
CM 38794–38799, 38801–38803 (paratypes)—Somalia.
- Eumecia anchietae wittei* Laurent, 1964, Serv. Cult. Comp. Diamantes Angola, 67:80.
CM 68377–68378 (paratypes)—Zaire.
- Gekko romblon* Brown and Alcala, 1978, Silliman Univ. Natur. Sci. Monogr., 1:75.
CM 60493 (paratype)—Philippines.
- Gerrhonotus liocephalus loweryi* Tihen, 1948, Trans. Kansas Acad. Sci., 51:302.
CM 41517 (paratype)—Mexico.
- Gerrhonotus lugoi* McCoy, 1970, Southwestern Nat., 15:37.
CM 49012 (holotype)—Mexico.
- Gymnodactylus agusanensis* Taylor (see McCoy and Richmond, 1966: 253).
CM P1949 (paratype)—Philippines.
- Leiocephalus barahonensis oxygaster* Schwartz, 1967, Tulane Stud. Zool., 14:36.
CM 40576 (paratype)—Republica Dominicana.
- Leiocephalus lunatus lewisi* Schwartz, 1969, J. Herpetol., 3:80.
CM 45867 (holotype), 45870–45874 (paratypes)—Republica Dominicana.
- Leiocephalus melanochorus hypsistus* Schwartz, 1965, J. Ohio Herp. Soc., 5:44.
CM 40551–40554 (paratypes)—Haiti.
- Leiocephalus personatus agraulus* Schwartz, 1967, Tulane Stud. Zool., 14:21.
CM 40570–40575 (paratypes)—Republica Dominicana.

- Leiocephalus personatus budeni* Schwartz, 1967, Tulane Stud. Zool., 14: 19.
CM 40566–40569 (paratypes)—Republica Dominicana.
- Leiocephalus personatus poikilometes* Schwartz, 1969, J. Herpetol., 3: 82.
CM 45868–45869 (paratypes)—Republica Dominicana.
- Leiocephalus personatus pyrrholaemus* Schwartz, 1971, Herpetologica, 27:178.
CM 52287 (holotype), 52288–52292 (paratypes)—Republica Dominicana.
- Leiocephalus personatus socoensis* Gali and Schwartz, 1982, J. Herpetol., 16:177.
CM 60543–60550 (paratypes)—Republica Dominicana.
- Leiocephalus personatus tarachodes* Schwartz, 1967, Tulane Stud. Zool., 14:11.
CM 40564–40565 (paratypes)—Republica Dominicana.
- Leiocephalus psammodromus aphretor* Schwartz, 1967, Ann. Carnegie Mus., 39:163.
CM 40602 (holotype)—Turks and Caicos Islands.
- Leiocephalus psammodromus apocrinus* Schwartz, 1967, Ann. Carnegie Mus., 39:165.
CM 40601 (holotype)—Turks and Caicos Islands.
- Leiocephalus psammodromus mounax* Schwartz, 1967, Ann. Carnegie Mus., 39:169.
CM 40603 (holotype)—Turks and Caicos Islands.
- Leiocephalus rhutidira* Schwartz, 1979, Proc. Biol. Soc. Washington, 92:273.
CM 60520 (holotype)—Haiti.
- Leiocephalus schreibersi nesomorus* Schwartz, 1968, J. Herpetol., 1:47.
CM 40595–40599 (paratypes)—Haiti.
- Lepidodactylus magnus* Brown and Parker, 1977, Proc. California Acad. Sci., 41:258.
CM 59037 (paratype)—Papua New Guinea.
- Liolaemus capillitas* Hulse, 1979, Ann. Carnegie Mus., 48:204.
CM 70114 (holotype), 70116–70117, 70119–70120, 70122–70138, 70140–70141, 70143–70144, 70146–70147 (paratypes)—Argentina.
- Lygosoma meleagris hackarsi* Witte, 1941, Expl. Parc Nat. Albert Miss. G. F. de Witte, 33:138.
CM 68380–68381 (paratypes)—Zaire.
- Mabuya perrotetii upembae* Witte, 1953, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 6:100.
CM 65465–65466 (paratypes)—Zaire.
- Mabuya quinquetaeniata pulcherrima* Witte, 1953, Expl. Parc Nat. Upemba Miss. G. F. de Witte, 6:103.
CM 65472–65473 (paratypes)—Zaire.

- Pachydactylus capensis katanganus* Witte, 1953, Expl. Parc Nat. Upemba Miss G. F. de Witte, 6:37.
CM 64495–64496 (paratypes)—Zaire.
- Pholidobolus macbrydei* Montanucci, 1973, Univ. Kansas Mus. Nat. Hist., Misc. Publ., 59:35.
CM 83708 (paratype)—Ecuador.
- Pholidobolus prefrontalis* Montanucci, 1973, Univ. Kansas Mus. Nat. Hist., Misc. Publ., 59:32.
CM 83709 (paratype)—Ecuador.
- Platysaurus imperator* Broadley, 1962, Occ. Papers Nat. Mus. So. Rhodesia, 3:816.
CM 58369–58370 (paratypes)—Zimbabwe.
- Platysaurus maculatus* Broadley, 1965, Arnoldia, 1(33):1.
CM 58351–58352 (paratypes)—Mozambique.
- Platysaurus pungweensis blakei* Broadley, 1964, Arnoldia, 1(5): 1.
CM 58361–58362 (paratypes)—Mozambique.
- Sphaerodactylus asterulus* Schwartz and Graham, 1980, Tulane Stud. Zool. Bot., 22:8.
CM 60521 (holotype), 60522–60536 (paratypes)—Haiti.
- Sphaerodactylus brevirostratus* Shreve, 1968, Breviora, 280:10.
CM 38882 (paratype)—Haiti.
- Sphaerodactylus clenchi* Shreve, 1968, Breviora, 280:21.
CM S8169 (paratype)—Republica Dominicana.
- Sphaerodactylus copei astreptus* Schwartz, 1975, Herpetologica, 31:4.
CM 56776–56781 (paratypes)—Haiti.
- Sphaerodactylus copei deuterus* Schwartz, 1975, Herpetologica, 31:5.
CM 56782 (holotype)—Haiti.
- Sphaerodactylus copei pelates* Schwartz, 1975, Herpetologica, 31:8.
CM 56783–56803 (paratypes)—Haiti.
- Sphaerodactylus corticola campter* Schwartz, 1968, Ann. Carnegie Mus., 39:237.
CM 40636 (holotype)—Bahamas.
- Sphaerodactylus corticola soter* Schwartz, 1968, Ann. Carnegie Mus., 39:232.
CM 40635 (holotype), 40630–40632 (paratypes)—Bahamas.
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THE ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA. IV. HABITAT SELECTION

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ABSTRACT

Distributional patterns in the small mammal fauna of the Caatinga were examined. Most of the caviomorph rodent and marsupial species preferentially utilize granitic outcroppings. Pronounced affinity for the stable, mesic granitic habitats evolved as an avoidance response to the unpredictable occurrence of extreme climatic conditions characteristic of the Caatinga. None of the murids exhibited this behavior.

INTRODUCTION

Background

When a species first invades a new region, it most likely selects the habitats most similar to those in which it has been successful through evolutionary time, especially if the previous selective pressures mandated strict adherence to a particular type of habitat. On the other hand, species occupying an area in which a new habitat develops have the opportunity to slowly adapt to the changing set of conditions; for example, the fossorial habits of the geomyids apparently developed in response to the gradual appearance of xeric habitat in North America (Russell, 1968). Because reduction of water stress is a primary consideration for small mammals in xeric areas, habitats which reduce water stress should be strongly favored, with species eventually developing pronounced affinities for these habitats. The rate of development of

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habitat selectivity will, however, be related to predictability of the environment; in xeric areas, timing and extent of rainfall are the critical elements. If water stress is continual or occurs at regular intervals within the life span of the animals, the environment must be tracked by individuals and rigorous natural selection processes will operate on each generation. Natural selection pressures operating on each generation will vary if severe environmental fluctuations occur only at intervals greater than individual life spans while intervening conditions are more moderate. The variability in natural selection pressures will thus decrease the overall rate of development of habitat specificity. At the species level then, habitat specificity and other related adaptations will accumulate slowly because individuals that select suboptimal habitat are not necessarily penalized, through shorter lifespans and less reproductive success, during moderate intervals when habitat of lower quality suffices. Subsequently, when the intermittent severe conditions and accompanying intense natural selection pressures reappear, populations occupying suboptimal habitat will be decimated. Invading, short-lived species should therefore find it especially difficult to adapt to an area where severe conditions occur only at widespread, irregular intervals.

The climatic regime of the Caatinga poses special problems for small mammal species. Although the area is generally semiarid, it is subject to both extremes of the precipitation spectrum, experiencing extended droughts and prolonged periods of heavy rainfall. The unpredictable occurrence of these disparate phenomena is a further confounding factor. Accumulation of specializations for the mean, semiarid environmental state will be extremely difficult or perhaps impossible for species occupying unstable Caatinga habitats because they are irregularly subjected to widely divergent selective pressures; the water conservation capabilities, foraging strategies, and predator-escape tactics favored in a sparsely-vegetated, arid environment are probably detrimental or of dubious value during mesic, thickly vegetated intervals. Small mammal species with origins in the surrounding, predictably mesic biomes should therefore require an extended period of time to develop a high degree of adaptation to the unusual climatic conditions which prevail in the Caatinga. A critical, mitigating factor is, however, present in the region; a large number of "microrefugia" exist. The abundant granitic outcroppings scattered throughout the area are relatively stable and mesic compared to the bulk of the Caatinga. The availability of these microrefugia has been of paramount importance in the adaptation of many Caatinga species.

The Caatinga

The current geographic boundaries of the Caatinga extend from 3° to 16° south latitude and from 35° to 45° west longitude, encompassing

an area of 650,000 km² (Reis, 1976; Frota-Pessoa et al., 1971). Although the Caatinga lies within the tropics, it is semiarid and experiences an unpredictable rainfall regime, thus deviating substantially from the bulk of tropical South America, which is relatively mesic and seasonally predictable. The rainfall regime is primarily influenced by the Southeast Trade Winds, in conjunction with three large, mobile masses of air. A general description of the climate can be found in Streilein (1982a), whereas a more detailed account of the patterns of rainfall and atmospheric circulation is available in Reis (1976) and Markham (1972). Each of the three moisture-laden air masses generally introduces some rain into the Caatinga in each year, but the amount of rain varies greatly from year to year, irregularly culminating in extended droughts and severe flooding. Three distinct geological features typify the Caatinga (Ab'Saber, 1970). A basement level of Precambrian crystalline rock, once covered by sedimentary rock, is now the dominant feature in the Caatinga, in terms of area encompassed. The surface layer of sedimentary rock has remained intact in certain areas, some of which are elevated above the surrounding countryside in the form of steep-sided plateaus (chapadas). The distinctive physiography of the Caatinga is attributed to the abundant, ubiquitous granitic formations; the sedimentary rock plateaus and extensive crystalline rock flats are relatively uniform and structurally simple compared to the granitic areas. Granitic rock occurs in the form of low mountain ranges (serras), small mountain ridges (serrotes), and lowland outcroppings (lajeiros). Structural diversity in the Caatinga on both local and geographic scales is primarily determined by the number, types, and distributional patterns of the granitic formations. Vegetation in the Caatinga ranges from relatively simple to extremely complex assemblages with regard to species abundance and composition, characteristic species, and foliage height profiles. In general, however, Caatinga vegetation can be classified into two largely distinct categories on the basis of foliage height profiles, with Caatinga Baixa (low thorn scrub) consisting of the various types of scrubby vegetation where canopy elements normally attain only 3 to 5 m, whereas Caatinga Alta (high thorn scrub) refers to vegetation types where the dominant canopy elements are typically greater than 5 m. Some of the granitic formations and sedimentary rock plateaus are elevated enough to function as orographic barriers and thus receive augmented rainfall. These areas (brejos) are able to sustain humid forests; the botanical affinities of the humid forests lie with the Atlantic Rain Forest (Andrade and Lins, 1964). A more comprehensive account of Caatinga geology and vegetation is contained in Streilein (1982a).

Most of the fieldwork for this project was done in the municipality of Exu in the northwestern corner of Pernambuco, Brazil. All of the three major geological features representative of the Caatinga are found in close proximity in that area. The dominant element, however, is the

Chapada do Araripe, an extensive sandstone plateau that stretches for hundreds of kilometers from east to west along the border of Pernambuco and Ceará. Numerous structurally complex granitic outcroppings, in the form of serrotes and lajeiros, are also present. The vegetation reflects the complexity of the area; the overall vegetation pattern may best be described as a mosaic of patches of variable size, some of which are clearly distinct while others gradually merge.

MATERIALS AND METHODS

Gross Habitat Utilization

Trapping and observations were conducted in each major habitat in the vicinity of Exu and on the Chapada do Araripe. Trapping records and field sites of AGGEU, a public health agency responsible for monitoring the small mammal species that harbor bubonic plague vectors, were examined for the municipality of Exu. Observations by AGGEU's professional collectors were also noted. Additional information was obtained during general mammal surveys in other parts of the Caatinga. A general treatment of distribution patterns for Caatinga mammals can also be found in Mares et al. (1980).

Microhabitat Utilization

A permanent, 12 by 12 (2.7 ha) live trapping grid was established at Fazenda Batente, 6 km SE of the town of Exu (7°31'S, 39°43'W), Pernambuco, Brazil. The grid encompassed portions of three distinct microhabitats. Sharply delineated microhabitats allowed each grid station to be classified in one of three categories—lajeiros (rock), Caatinga Baixa (low thorn scrub), or old field. Individual capture locations were recorded for the eight species captured between December 1976 and February 1978. Chi-square tests were performed to determine if the species were utilizing the microhabitats in proportion to their frequency of occurrence on the grid. In several instances, the low thorn scrub and old field categories were combined because the number of expected captures in the old field was too small to satisfy the requirements of the Chi-square test.

RESULTS

Gross Habitat Utilization

The occurrence of species in each major Caatinga habitat is summarized in Table 1; however, some of the relationships between species and habitats require further clarification. Both *Monodelphis domestica* and *Didelphis albiventris* are ubiquitous, but population densities are greatest in the granitic outcroppings. The other marsupial, *Marmosa karimii*, was extremely rare. It is known to occur only in thorn scrub and the latter seral stages of old field succession, but may occasionally utilize other habitats. *Wiedomys pyrrhorhinos* is the only widespread murid species. *Oryzomys eliurus* and *O. subflavus* occupy the habitats listed in Table 1 only in the immediate vicinity of the Chapada do Araripe; *Calomys callosus* also has a very restricted distribution. *Bolomys lasiurus* extends somewhat further into the Caatinga proper but populations are very localized. *Galea spixii* does occur in Caatinga Baixa, but individuals are concentrated at the interfaces with agricul-

Table 1.—*Habitat types utilized by Caatinga small mammals.*

Species	Naturally occurring				Agriculture	
	Granitic outcroppings		Caatinga		Cultivated fields	Abandoned fields (in suc- cession)
	Lajeiros	Serrotos	Baixa	Alta		
Marsupialia						
Didelphidae						
<i>Monodelphis domestica</i>	X	X	X	X	X	X
<i>Marmosa karimii</i>	?	?	X	?	?	X
<i>Didelphis albiventris</i>	X	X	X	X	X	X
Rodentia						
Muridae						
<i>Oryzomys eliurus</i>					X	
<i>Oryzomys subflavus</i>					X	
<i>Bolomys lasiurus</i>					X	X
<i>Calomys callosus</i>			X			X
<i>Wiedomys pyrrhorhinos</i>			X			
Caviidae						
<i>Kerodon rupestris</i>	X	X				
<i>Galea spixii</i>	X		X		X	X
Echimyidae						
<i>Thrichomys aperoides</i>	X	X				

turally derived habitats; extensive stands of low thorn scrub are virtually devoid of *G. spixii*.

Examination of Table 1 reveals three significant trends. First, murids are totally lacking in the relatively mesic, granitic outcroppings. Second, three of the five murid species (*B. lasiurus* and both species of *Oryzomys*) are found only in habitats created by agricultural practices. Third, the only species restricted to the granitic outcroppings are both caviomorph rodents, one caviid (*Kerodon rupestris*) and one echimyid (*Thrichomys aperioides*).

Microhabitat Utilization

None of the six species examined, on the basis of total captures, utilized the microhabitats with respect to proportion of occurrence on the grid (Table 2). While *K. rupestris* did not readily enter traps, visual observations followed a similar pattern, with sightings concentrated in structurally-complex boulder strewn areas (Lacher, 1981; personal observation). Three species, *M. domestica*, *D. albiventris*, and *T. aperioides*, disproportionally frequented the traps in rocky areas. The largest percentage of the variance in *G. spixii* microhabitat usage re-

Table 2.—Results of Chi-square tests on microhabitat utilization on the grid based on total captures. The (+) denotes a substantial portion of the variance which is due to greater-than-expected utilization. (−) denotes the converse relationship.

Species	Microhabitats			Total
	Rock	Thorn Scrub	Old Field	
Marsupialia				
Didelphidae				
<i>Monodelphis domestica</i>				
Observed	112	17	6	135
Expected	67.8	59.3	8.0	
χ^2	28.8	30.2	0.5	59.5***
% Variance	48.4 (+)	50.8 (−)	0.8 (−)	$P \ll .001$
<i>Didelphis albiventris</i>				
Observed	151	85	15	251
Expected	126.0	110.2	14.8	
χ^2	5.0	5.8	0.0	10.8**
% Variance	46.3 (+)	53.7 (−)	0.0	$P < .01$
Rodentia				
Muridae				
<i>Bolomys lasiurus</i>				
Observed	0	12		12
Expected	6.0	6.0		
χ^2	6.0	6.0		12.0***
% Variance	50.0 (−)	50.0 (+)		$P < .001$
<i>Calomys callosus</i>				
Observed	1	16		17
Expected	8.5	8.5		
χ^2	4.8	4.8		9.6**
% Variance	50.0 (−)	50.0 (+)		.01 < $P < .001$
Caviidae				
<i>Galea spixii</i>				
Observed	66	32	16	114
Expected	57.2	50.0	6.7	
χ^2	1.4	9.7	10.3	21.4***
% Variance	6.5 (+)	45.3 (−)	48.1 (+)	$P < .001$
Echimyidae				
<i>Thrichomys apereoides</i>				
Observed	731	77	14	822
Expected	412.6	360.9	48.5	
χ^2	245.7	223.9	24.5	493.5***
% Variance	49.8 (+)	45.2 (−)	5.0 (−)	$P \ll .001$

Table 3.—Microhabitat utilization by the caviomorph rodents, *Galea spixii* and *Thrichomys apereoides*, during wet and dry months on the grid. Months were classified as wet if mean monthly temperature in °C < ½ × mm rainfall/month.

Species	Microhabitats			Total
	Rock	Thorn Scrub	Old Field	
Caviidae				
<i>Galea spixii</i>				
Wet				
Observed	21	11		32
Expected	16.0	16.0		
χ^2	1.6	1.6		3.2 ns
% Variance				.1 < P < .05
Dry				
Observed	45	24	13	82
Expected	41.6	35.3	5.2	
χ^2	0.3	3.6	11.7	15.6***
% Variance	1.9 (+)	23.1 (-)	75.0 (+)	P < .001
Echimyidae				
<i>Thrichomys apereoides</i>				
Wet				
Observed	189	27	1	217
Expected	108.5	96.1	12.4	
χ^2	59.7	49.7	10.5	119.9***
% Variance	49.8 (+)	41.5 (-)	8.8 (-)	P ≤ .001
Dry				
Observed	542	50	13	605
Expected	306.7	260.2	38.1	
χ^2	180.5	169.8	16.5	366.8***
% Variance	49.2 (+)	46.3 (-)	4.5 (-)	P ≤ .001

sulted from the concentration of captures in the old field trap stations, and the underrepresentation in thorn scrub stations. Old field and thorn scrub categories were combined for *B. lasiurus* and *C. callosus* because the total number of captures was small; all of the *B. lasiurus* captures in the combined category were actually in the old field and those of *C. callosus* were all in the thorn scrub. The mixed category was much preferred over the rocky microhabitat.

Comparison of microhabitat utilization in wet versus dry months, based on months with relative water surpluses or deficits (Streilein, 1982a), revealed trends (Tables 3–4) obscured in the analysis of total captures. *Monodelphis domestica* and *T. apereoides* captures remained concentrated in the rocky areas in both wet and dry months. *Bolomys lasiurus* and *C. callosus* could not be compared in this man-

Table 4.—*Microhabitat utilization by the marsupials, Monodelphis domestica and Didelphis albiventris, during wet and dry months on the grid. Months were classified as wet if mean monthly temperatures in °C < ½ × mm rainfall/month.*

Species	Microhabitats			Total
	Rock	Thorn Scrub	Old Field	

<i>Monodelphis domestica</i>				
Wet				
Observed	44		10	54
Expected	27.0		27.0	
χ^2	10.7		10.7	21.4***
% Variance	50.0 (+)		50.0 (−)	$P < .001$
Dry				
Observed	68	8	5	81
Expected	41.1	34.8	5.1	
χ^2	17.6	20.6	0.0	38.2***
% Variance	46.1 (+)	53.9 (−)	0.0	$P \ll .001$

<i>Didelphis albiventris</i>				
Wet				
Observed	33		25	58
Expected	29.0		29.0	
χ^2	0.6		0.6	1.2 ns
% Variance				.3 < P < .2
Dry				
Observed	118	62	13	193
Expected	97.2	83.0	12.2	
χ^2	4.2	5.3	0.0	9.5**
% Variance	44.2 (+)	55.8 (−)	0.0	$P < .01$

ner because the number of captures in each category did not provide an adequate sample size. Both *G. spixii* and *D. albiventris* exhibited distributions of captures proportional to the frequency of occurrence of microhabitats during the months with relative water surpluses. Captures in dry months, however, were not proportionally distributed; *D. albiventris* favored rocky areas and avoided thorn scrub while *G. spixii* was trapped much more often in the old field than was expected (75% of the variance).

DISCUSSION

The major types of habitats which naturally occur in the Caatinga are serrotes and lajeiros, Caatinga Alta, and Caatinga Baixa. A large area is currently covered by abandoned fields in various stages of succession (the result of slash and burn agriculture) and a smaller area is claimed each year from Caatinga Alta and Baixa habitats for agricultural purposes. These habitats encompass a rough moisture gradi-

ent, with serrotes and lajeiros being the most mesic, followed by Caatinga Alta, and finally Caatinga Baixa. The small mammals which inhabit the granitic outcroppings acquire two important advantages. First, even a light rain forms temporary pools in depressions in the rock as a result of runoff from more elevated surfaces; these ephemeral sources of free water are of paramount importance because the Caatinga is devoid of permanent streams. Second, some of the runoff percolates into cracks and fissures; this water is slowly lost to the atmosphere, thus maintaining higher relative humidity in the outcroppings.

The zoogeographic theories advanced by Patterson and Pascual (1968, 1972), Hershkovitz (1966, 1969, 1972), and Marshall (1979) basically agree that marsupials and caviomorph rodents were in South America long before the murids arrived. It is conceivable then that representatives of these groups could have already been occupying the area in which the Caatinga eventually arose, affording them the opportunity to adapt as environmental conditions gradually changed. Alternatively most of the species may still have invaded the Caatinga much earlier than the murids. In either case, they have generally had a longer period of time to adjust to the area and should thus exhibit a higher degree of adaptation.

Small mammals in xeric areas should theoretically select habitats which reduce water stress unless they are particularly well adapted to an arid environment. In the Caatinga, then, most species might be expected to inhabit serrotes and lajeiros. The observed distributional patterns for marsupials and caviomorph rodents generally followed this pattern; all of the common caviomorphs and marsupials utilized the granitic outcroppings to a large degree. *Kerodon rupestris* and *T. aperioides* were virtually limited to the immediate vicinity of the outcroppings, *M. domestica* populations were primarily concentrated in the rock-dominated habitats, and *D. albiventris* rapidly responded to the occurrence of relative water deficits by preferentially utilizing the outcroppings. The caviomorph, *G. spixii*, was the only species that did not exhibit highly preferential usage of the granitic outcroppings, even in intervals of severe water stress. *Galea spixii* did use the rocky habitats, so it was not a situation where the habitat was inaccessible or hostile. The observed pattern of distribution apparently resulted from *K. rupestris* actively excluding any *G. spixii* individuals encountered. *Kerodon* reacted aggressively and clearly established dominance over the much smaller *Galea* in behavioral trials in neutral arenas (Streilein, 1982d) and in three mixed-colony situations (Lacher, 1981). The most significant aspect of the situation is that none of the common species of the two groups that should have had the greatest amount of time to adapt to the Caatinga preferentially utilized Caatinga Baixa, the most extensive habitat-type available. All of them did, how-

ever, utilize the most stable, mesic habitat-type available, the granitic outcroppings.

Examination of two of the caviomorph species suggests that they may antedate the Caatinga or at least have invaded it at a very early date. *Kerodon rupestris* is the only representative of the ecologically and behaviorally diverse rodent family, Caviidae, with a distribution limited to rocky areas. This species also has morphological, rock-dwelling adaptations, leathery pads on the feet and subcutaneous nails on all digits but the innermost digit of the pes, unique to the subfamily Caviinae (Lacher, 1981). Fifteen genera are currently recognized in the Echimyidae (Walker, 1975), but of the approximately 70 species in this family, only *T. apereoides* is known to exist in a xeric area. *Thrichomys apereoides* is also distributed solely in areas dominated by rock outcroppings. This affinity for rocks is pronounced; populations in the Cerrado biome are also found only in the limited number of rocky areas (T. E. Lacher, Jr., personal communication) as are the populations in the Chaco in Paraguay (P. Myers, personal communication). These disjunct populations were probably established when the Caatinga expanded during the dry phases of the Quaternary climatic cycles. The uniqueness of *Kerodon* and *Thrichomys* with regard to their respective congeners, considered in conjunction with the special attributes of the Caatinga biome, suggests a very ancient relationship.

The absence of the murid rodents from the granitic outcroppings in the Caatinga is in stark contrast with the distribution patterns of the common caviomorph rodents and marsupials. Hershkovitz (1972) and Marshall (1979) contend that the immigration of murids commenced in the Miocene, whereas Patterson and Pascual (1972) propose arrival at the Pliocene-Pleistocene junction. If the murids did arrive in the Miocene, they have had ample time to disperse to the Caatinga; expansions of the Caatinga biome far into the Amazon valley during the Quaternary climatic cycles should have increased the probability of contact. The area currently occupied by neighboring biomes, primarily the Cerrado in the west and southwest and to a lesser extent, the Palm Forest in the northwest, does not, however, possess the numerous granitic outcroppings characteristic of the Caatinga. The narrow strip of Atlantic Rain Forest to the east does contain outcroppings, but the fauna of the Caatinga contains more elements in common with that of the Cerrado (Streilein, 1982a). Invading murid species are much more likely to have approached the Caatinga through an area lacking rocky habitats and thus did not have the opportunity to develop a habitat affinity that would have preadapted them for existence in the unpredictable environment of the Caatinga. The principal habitats occupied

by *C. callosus*, *B. lasiurus*, and *O. eliurus* in the Cerrado included fields of felled trees with pastures, open scrub with herbs and grass, and early successional fields, whereas *O. subflavus* is found in all types of natural habitats but is rare in the open grassland (Mello, 1977). The limited number of habitats occupied by murids in the Caatinga are all strikingly similar to some of the primary habitats occupied by these species in the Cerrado.

The particular problems imposed by the climatic regime of the Caatinga may be invoked to explain why the murids continue to occupy habitats in the Caatinga similar to those occupied in the Cerrado, but which are much more unstable. Irregular subjection to widely divergent selection pressures in the thorn scrub habitats, operating in conjunction with the lack of a previously established affinity for rocky habitats, may effectively preclude both possible solutions—shifting habitat preference in favor of the granitic outcroppings or accumulation of specializations for existence in the thorn scrub. The absence of the murids from the granitic outcroppings does not appear to be related to morphological limitations as most of the murids are as capable of climbing as the morphologically general marsupials. An alternative hypothesis is that the murids may simply not have had a sufficient amount of time to adapt. The retention of affinity for habitats similar to those occupied in the Cerrado, the absence from the most stable, mesic habitats available, the inability to maintain the high population levels characteristic in the Cerrado (Streilein, 1982c), and the poorly developed water conservation capabilities of some of the species (Streilein, 1982b) indicate that the murids, in general, have not achieved a high degree of adaptation, but this situation can be attributed to either hypothesis. Two additional factors must also be considered. First, *Galena spixii* utilizes the granitic outcroppings in the Caatinga to some extent and has a broad distribution in open formations throughout South America, including broad expanses that lack rock outcroppings. Second, *Wiedomys pyrrhorhinos* is the only murid rodent that has a broad geographic distribution in the Caatinga and is the only small mammal species found only in Caatinga Baixa habitats. The preference for thorn scrub habitats suggests that *Wiedomys* is evolving into a true thorn scrub specialist, at least within the realm of constraints imposed by the climatic vagaries. Development of a high degree of specialization for the “mean” semiarid state may, in fact, be precluded by the disparate selection pressures. These two factors suggest that the alternative hypothesis is correct, with the major effect of the conditions incorporated into the first hypothesis being to prolong the transition.

The occurrence of most of the murid species in this portion of the Caatinga can be attributed to the presence of the Chapada do Araripe,

Cerrado biome that stretches unbroken through nearly three-fourths of the width of the Caatinga. Extant populations may be relicts of the most recent expansion of the Cerrado into the area currently occupied by the Caatinga, or the Chapada do Araripe may have served as an invasion corridor into the Caatinga. In either case, current distributions might be expected to be limited to the Chapada and immediate vicinity because microclimatic and vegetation differences rapidly become more pronounced with increased distance into the Caatinga proper. The observed distributional patterns of *Calomys callosus* and both species of *Oryzomys* were, in fact, restricted; individual *C. callosus* were encountered less frequently with increasing distance from the base of the Chapada, disappearing entirely after 15 to 20 km, whereas both *Oryzomys* species extended no more than 5 to 10 km into the Caatinga. *Bolomys lasiurus* was most abundant in sites next to the Chapada, but may be found at suitable localities more distant than 20 km from the Chapada. The outlying populations of *Bolomys lasiurus* were probably founded by emigrants from temporarily dense populations.

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THE ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA. V. AGONISTIC BEHAVIOR AND OVERVIEW

KARL E. STREILEIN¹

ABSTRACT

Basic agonistic behavior repertoires are described for Caatinga species. The results of interspecific encounters suggest that behavioral interactions contribute to the maintenance of observed distributional patterns; *Galea spixii* is actively excluded from granitic habitats by *Kerodon rupestris*.

Analyses of water conservation capabilities, reproductive and population parameters, and distribution patterns indicate that the caviomorph rodents and marsupials, in general, exhibit a higher level of adaptation to the Caatinga than do the murid rodents.

INTRODUCTION

A comprehensive study of a small mammal community must explore the possibility that interspecific behavioral interactions influence distributional patterns. Within a community, interspecific interactions may range from overt unidirectional aggression or mutual intolerance to unilateral, active avoidance or mutual avoidance. MacMillen (1964) and Bateman (1967) documented the existence of dominance hierarchies in two rodent faunas in xeric areas of North America. The hierarchies were generally correlated with body size of the constituent species and were maintained with a minimum of overt aggression. Heller (1971) and Terman (1974), on the other hand, examined situations in which overt aggression was commonplace. Although the mechanism may vary, a similar result is obtained; a species can be partially

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or completely excluded from a particular area or by another species. This process may be viewed as one of the many forms of competition.

In the Caatinga, as in any other xeric region, habitats with favorable water balance are limited and by logical extension, should be focal points for competitive interactions. MacMillen's (1964) study of the rodent fauna of a semiarid area confirmed the impact of interspecific behavioral relationships under these conditions. Most of the species studied were dependent upon patches of cacti (*Opuntia occidentalis*) as a water source, but the socially dominant species (*Neotoma lepida*) excluded subordinate species from the water-rich patches. It was expected that a similar process might occur in the Caatinga, with living space in the granitic outcroppings being the limited resource. Granitic outcroppings in the Caatinga serve as relatively mesic, stable micro-refugia that moderate both the mean, xeric environmental conditions and the unpredictable occurrence of intervals of extended drought.

Different degrees of agonistic interactions were anticipated in the interspecific encounters. Because *Galea spixii* and *Kerodon rupestris* were closely related, both phylogenetically and ecologically, they were expected to exhibit the most intense agonistic behavior. No overt aggression, but possibly some type of avoidance response, was anticipated between *Thrichomys apereoides* and *Galea spixii* or *T. apereoides* and *K. rupestris* because these pairs were quite different in activity patterns, and taxonomic affinities. Habitat selection by *Bolomys lasiurus* appeared to be determined by factors other than exclusion by another species, so few or no interactions were expected between *T. apereoides* and *B. lasiurus*.

MATERIALS AND METHODS

The qualitative analysis of behavior commenced with an attempt to describe the basic behavioral repertoire of each species. Individuals were isolated in glass- or screen-fronted observation cages to study maintenance and exploratory behavior. Social interactions were then observed in male-male, male-female, and female-female pairs. Family units were also observed when possible. Agonistic, sexual, marking, and grooming displays and postures were the primary areas of interest.

These components were then quantified in intraspecific social interactions, within the context of staged encounters in neutral arenas. Varying sizes of arenas were used depending on average body size of each species: *Bolomys lasiurus* and *Oryzomys subflavus*, 0.4 m²; *Monodelphis domestica*, 0.8 m²; and *Galea spixii* and *Thrichomys apereoides*, 1.4 m². External reproductive condition of test animals was recorded in order to isolate possible effects of reproductive status. To reduce artifacts produced by prolonged confinement, trials were limited to five minutes; all individuals used were wild-caught adults maintained in the lab for several weeks before testing. The number of trials in each species ranged from 40 (*Monodelphis*) to 117 (*Bolomys*). Two individuals were simultaneously released and a record made of actions following the first encounter.

Finally, interspecific interactions among rodent species were studied; marsupial species were excluded from this phase as interactions were likely to be of a predator-prey nature. Only those species which occurred on the grid were used. The primary objective was

interactions between rock dwelling species, so trials were conducted as follows: *Thrichomys* versus *Galea*; *Thrichomys* versus *Kerodon*; and *Galea* versus *Kerodon*. *Thrichomys apereoides* was also tested against *Bolomys lasiurus*. Twenty 5-min trials were conducted in each category. Ten males of one species were matched with five males and five females of the other species and ten females were also matched with an equal number of males and female. This system was adopted to minimize possible sex-related differences in the interactions.

INTRASPECIFIC AGONISTIC BEHAVIOR

The basic components of the agonistic behavioral repertoire of each species are presented in Table 1. *Didelphis albiventris* and *Galea spixii* are the only species which lack upright postures. Relative differences rather than absolute differences in behavioral patterns must also be considered (Eisenberg, 1967). The frequency of utilization of various components was quite variable within species. Infrequently observed events were sometimes very important in the context in which they occurred. Because individual variation was large and the frequency with which events occurred was dependent upon the actions of both individuals in a trial, description of displays, movements, and postures and the context in which they generally occur are given only for species with a substantial number (>40) of trial encounters. The data presented in Tables 2–5 reflect both aggression and active defense. Typical sequences of behaviors and agonistic displays and postures are portrayed for *M. domestica* (Figs. 1–2), *B. lasiurus* (Figs. 3–4), *G. spixii* (Figs. 5–6), and *T. apereoides* (Figs. 7–8).

Displays and Postures of Monodelphis domestica

Open mouth threat.—The prominence of this display varies directly with the intensity of the situation. At a low level, the jaws are only slightly open and only the canines are obviously exhibited. At a high level of intensity, the jaws gape and the lips are drawn back, exposing all of the teeth. Open mouth threats are observed in all postures.

Quadrupedal.—Defensive or aggressive lunges may originate while the animal is in the basic quadrupedal stance.

One forepaw raised.—A single forepaw is flexed and held roughly parallel to the ground but close to the chest. This is generally observed only in animals being approached. Animals which assume this posture are more likely to employ an active defense than to flee.

Semi-erect.—Both forepaws are flexed and held parallel to the ground. This posture is similar to the position adopted by most individuals during feeding bouts and is easily maintained for long periods. Approaching animals frequently enter this posture before attacking, while in individuals being approached, it signals an imminent defensive strike. The chief advantage of this upright posture to these otherwise largely quadrupedal animals appears to be a more favorable angle of

Table 2.—Frequency of agonistic behavior components for *Monodelphis domestica*. Means based on total trials for each class. No. = number of trials in which each component occurred. MPT = mean per trial. ¹Total number of trials in which agonism occurred/total number of trials.

Components	Classes							
	$\delta\delta$ 13/16 ¹		$\delta\delta/\text{♀♀}$ 14/6		♀♀ 8/8		Total 35/40	
	No.	MPT	No.	MPT	No.	MPT	No.	MPT
Open mouth	12	2.6	14	3.8	8	5.0	34	4.0
One forepaw up	2	0.1	1	0.1	1	0.1	4	0.1
Semi-erect	3	0.3	6	0.5	2	0.4	11	0.4
Full erect			3	0.3	2	0.4	5	0.2
Chase	2	0.4	1	0.1	4	1.0	7	0.4
Bite	5	0.9	5	0.4	4	1.3	14	0.8
Wrestle	2	0.2	2	0.1	4	1.1	8	0.4
Lunge	6	0.5	4	0.4	5	1.5	15	0.7
Strike with forepaws	1	0.1	3	0.3	1	0.1	5	0.2
Spar			4	0.3	1	0.1	5	0.2

attack; the opponent is less likely to effectively use its canines in an upward direction.

Full erect.—This posture is of very brief duration and invariably precedes an extended lunge. The flexed forepaws are raised above the shoulders as the animal throws itself forward and down onto the opponent.

Lunge.—The body is hurled forward at the opponent. Forepaws function more in grabbing the opponent prior to administering a bite than as striking weapons.

Wrestle.—Biting is common. The nails on the hindfeet are used to rake the opponent.

Agonistic behavior was recorded in 35 of 40 trials (Table 2). Individuals were intolerant of other individuals in close proximity regardless of sex. Open mouth threats were frequently observed and were generally successful at inhibiting approaching animals. When physical contact did occur, it was usually of brief duration and rarely resulted in serious injury.

Displays and Postures of Bolomys lasiurus

Open mouth threat.—The jaws gape and the lips are drawn away from the teeth. This display denotes either an inclination to attack (when given by an approaching animal) or a willingness to engage in active defense (when given by an animal being approached). It is typically given in conjunction with all of the postural displays.

One forepaw raised.—This posture is an intermediate stage between

Table 4.—Frequency of agonistic behavior components for *Galea spixii*. Means based on total trials for each class. No. = number of trials in which each component occurred. MPT = mean per trial. VO = vagina open; VC = vagina closed; TD = testes descended; TND = testes not descended. ¹Number of trials in which agonism occurred/total number of trials. ²Average based on two trials.

[illegible]

Table 5.—*Frequency of agonistic behavior components for Thrichomys apereoides. Means based on total trials for each class. No. = number of trials in which each component occurred. MPT = mean per trial. TND = testes not descended; VO = vagina open; VC = vagina closed. ¹Total number of trials in which agonism occurred/total number of trials.*

Components	Classes									
	Females 4/18 ¹		TND × TND 7/14		TND × VC 5/14		TND × VO 5/13		Total 21/59	
	No.	MPT	No.	MPT	No.	MPT	No.	MPT	No.	MPT
Semi-erect	3	0.8	3	0.4	2	0.5	4	0.4	12	0.5
Full erect	3	0.5	4	1.1	4	0.6	1	0.1	12	0.6
Strike with forepaws	1	0.1	3	0.3	2	0.1	1	0.1	7	0.1
Spar			2	0.2					2	0.1
Locked upright	3	0.2	3	0.4	4	0.3			10	0.2
Chase			2	0.2			1	0.1	3	0.1
Lunge	1	0.1	1	0.2	1	0.1	1	0.1	4	0.1
Bite	1	0.1	4	0.4	1	0.1	2	0.2	8	0.2
Chest kick	2	0.1	3	0.4	2	0.1			7	0.2

quadrupedal and upright postures and denotes slightly increased intensity. Animals may immediately progress into an upright posture without exhibiting this posture.

Semi-erect.—This posture has several functions. It signals a high probability of active defense to an intruder, typically a forward and downward lunge with a blow delivered by both forepaws; it often stops or delays the advancing animal. If the animal being approached is bluffing, as is often the case when subordination had been determined by previous encounters, it takes advantage of the intruder's hesitation to leap away. When the approaching animal assumes this posture, an attack is likely to occur.

Full erect.—When assumed in defense by an animal being approached, the probability of a defensive strike is close to 100% if the approach continues. Full erect by an approaching animal frequently provokes flight or is the immediate precursor to an aggressive strike. Alternatively, both individuals may opt for the alternate vertical stretches sequence and avoid physical contact.

Alternate vertical stretches.—First one individual stretches vertically into a more pronounced full erect, then the other does so, and so forth. The individual with the maximum stretch holds it and the other animal slowly drops in stages back to the quadrupedal stance and moves off. The stretching sequence is sometimes repeated one or more times before the outcome is determined. Because increasing body

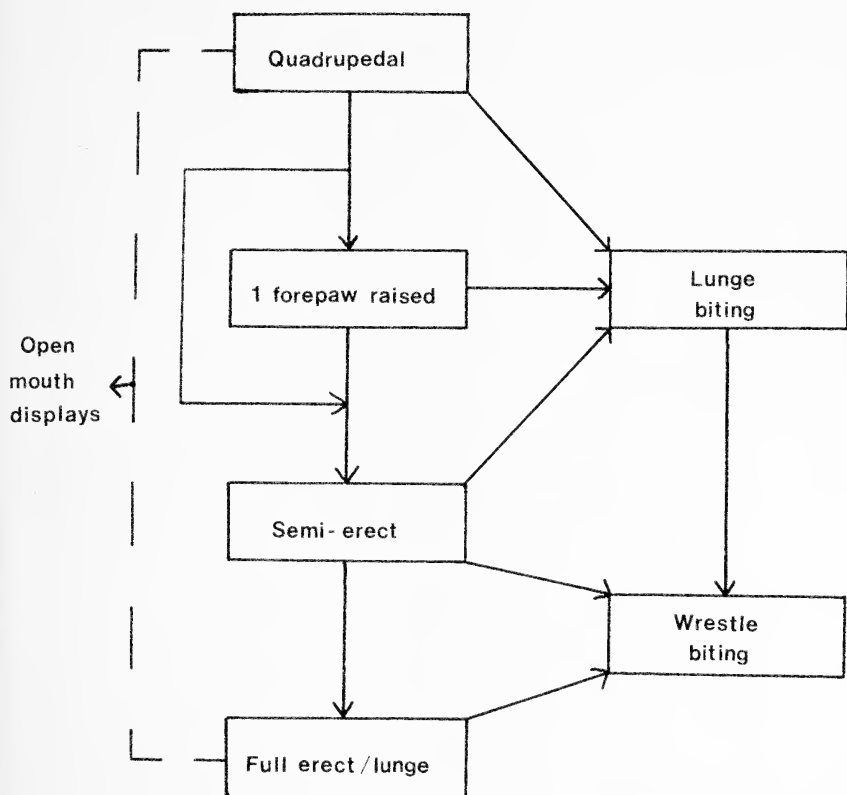


Fig. 1.—Agonistic behavior sequences for *Monodelphis domestica*. Open mouth displays occur in all postures.

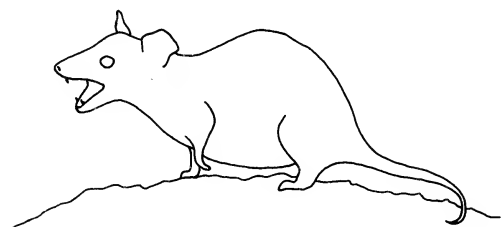
length is directly related to increasing body weight, the opponents can gauge each other's size (and presumably strength) and settle an encounter without engaging in physical contact.

Circling.—In extended aggressive bouts, mutual circling sometimes occurs when both individuals are in semi-erect or full erect postures. Circling is of variable duration but is apparently an attempt to maneuver into a position with a more advantageous angle for attacking.

Strike with forepaws.—Blows are typically directed at the head of the opponent with the forepaws raked over the eyes. This tactic is used from semi-erect and full erect postures. In a defensive context, the blow is given quickly and the animal maintains its position, often drawing back into the ready position. In the agonistic context, striking



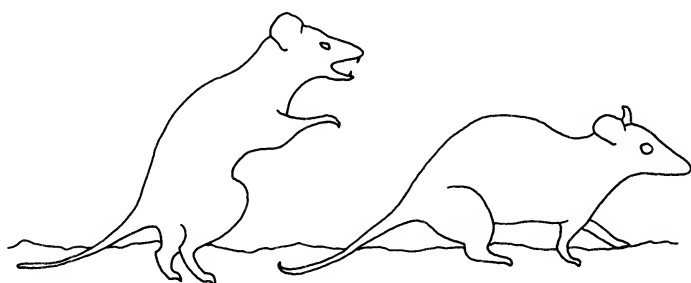
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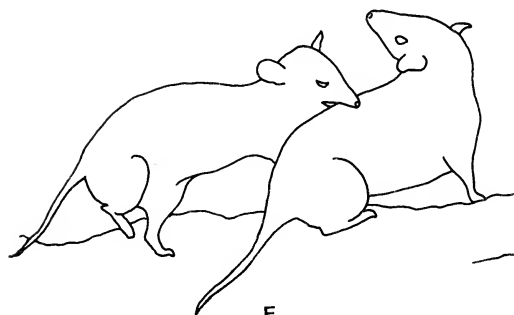
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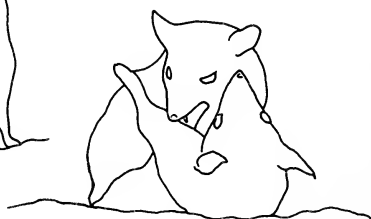
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E



F

with the forepaws is more often the culmination of an extended lunge at the opponent.

Kick with one rear paw.—The animal hops past the opponent's side and kicks out laterally with a rear paw. This tactic was most frequently observed during extended, mutually aggressive encounters and is most often used from the circling mode.

Wrestle.—Animals are usually stomach to stomach and on their sides. Hind feet are used to rake the opponent's abdomen.

Chase.—Active pursuit of a fleeing individual. Chases are generally terminated after the fleeing animal is caught and bitten.

Agonistic behavior was observed in 90 of 117 trials (Table 3). Open mouth threats and the semi-erect posture were the most frequently used components. Physical contact between opponents was common but serious injuries were rare. In the majority of trials, mutual intolerance was the rule.

Displays and Postures of Galea spixii

Quadrupedal.—Attacks may be precipitated from the basic quadrupedal stance.

Arch.—The back is arched somewhat as the entire body is held higher off the ground. The body may curl (on the lateral plane) during this display. This posture advertises an inclination toward active defense when given by an animal being approached. It also serves as an indicator that an attack is probable when exhibited by an approaching animal.

Stiff-legged hop.—This posture is essentially the same as the arch posture, but the animal bounces directly toward the opponent or parallel to it. Apparently, it conveys a high intensity message because in the relatively few times it was observed, a fleeing response was invoked in the opponent before any physical contact was made.

Piloerection.—This display may accompany any of the postures. The pelage along the mid-dorsal line is usually raised but the phenomenon may extend over much of the dorsal surface.

Open mouth threat.—The mouth is held open to varying degrees and the lips are drawn away, further exposing the teeth. This display is frequently observed in all postures.

←

Fig. 2.—Agonistic displays and postures for *Monodelphis domestica* depicting defensive actions by the animal on the right when approached by a conspecific: open mouth display (A), raising one forepaw (B), and assuming the semierect posture (C). In (D), the defensive response escalates into a lunge from the full erect posture when the intruder approaches too closely, followed by biting the intruder (E). A wrestling bout ensues (F).

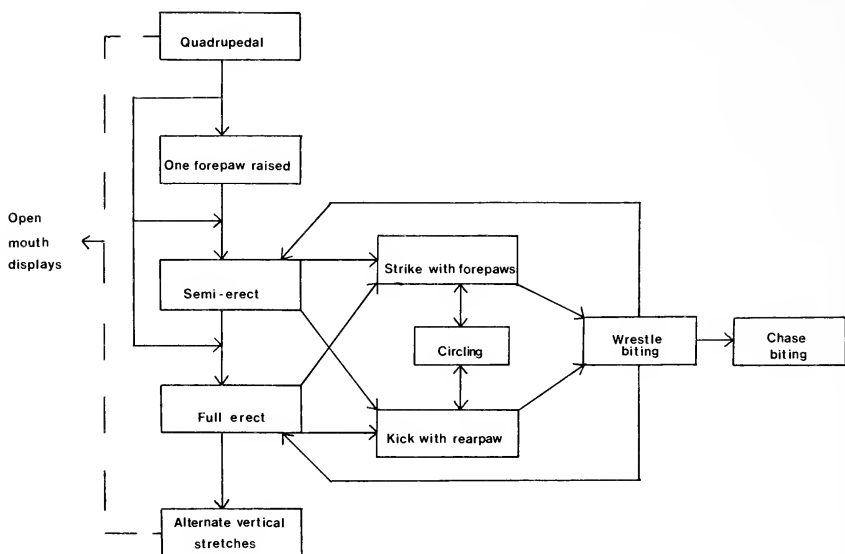


Fig. 3.—Agonistic behavior sequences for *Bolomys lasiurus*. Open mouth displays are common in all postures. Striking and kicking occur intermittently while the animals circle one another.

Lunge.—This tactic is most frequently used when the animals are in close proximity. The entire body is hurled at the side or hindquarters of the opponent. It may be used in longer range situations to signify agonistic intent and often provokes immediate flight in a subordinate animal.

Run at.—This tactic is used only in active aggressive attacks. An animal runs at full speed toward its opponent, ramming into its side if the opponent does not flee.

Wrestle.—Bouts are usually of brief duration. Biting is common and the rear legs are used extensively.

Chase.—Pursuit is often prolonged, with continuous biting of the rump. Agonistic chases are similar in form to mating chases but the bites directed at the rump are much more intense.

Agonistic behavior was observed in 59 of 108 trials (Table 4). Female-female encounters accounted for more than one-half of the aggressive behavior. Most of the agonistic behavior in male-male trials was initiated because one male reacted aggressively after the other initiated sexual activity.

Display and Postures of Thrichomys apereoides

Semi-erect.—The forepaws are drawn up to shoulder height and flexed. A defensive strike is probable if an approaching animal contin-

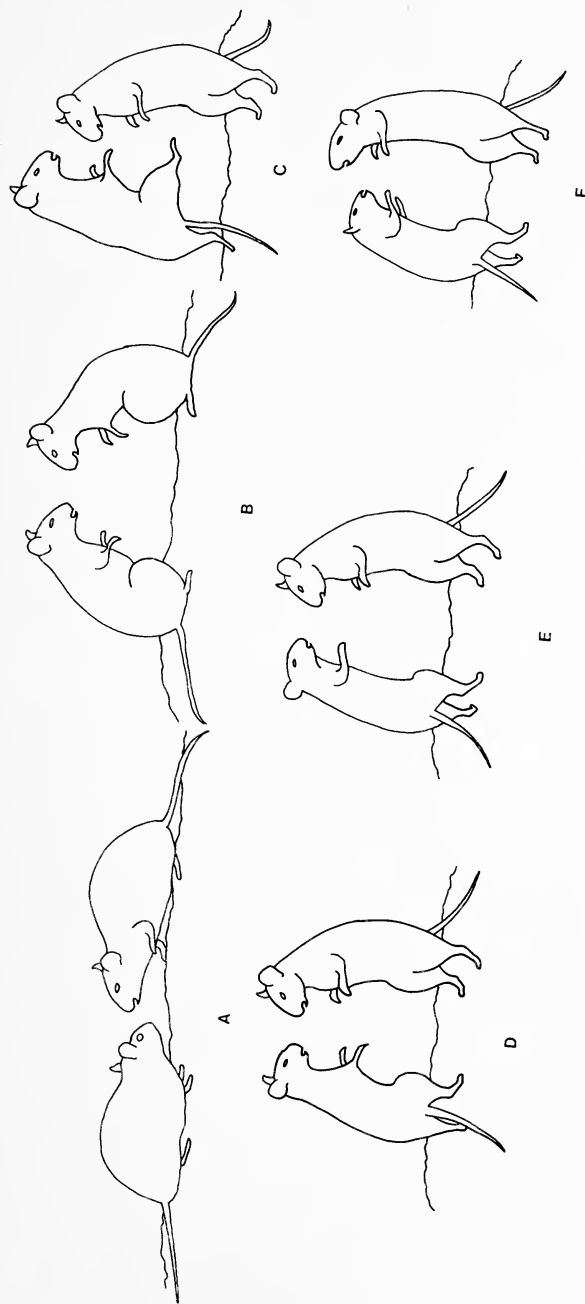


Fig. 4.—Agonistic displays and postures for *Bolomys lasiurus*. The animal on the right is in a low intensity defensive posture with one forepaw raised while exhibiting an open mouth display (A); both animals assume the semi-erect posture (B); the animal on the left jumps and kicks at the opponent with one rear paw (C). The alternate vertical stretch sequence is initiated in (D) as the animal on the right stretches higher, followed by the opponent's stretch in response (E). The sequence is completed in (F) when the animal on the right attains a greater height with its stretch, thus winning the encounter without physical contact; its opponent begins to twist down and away.

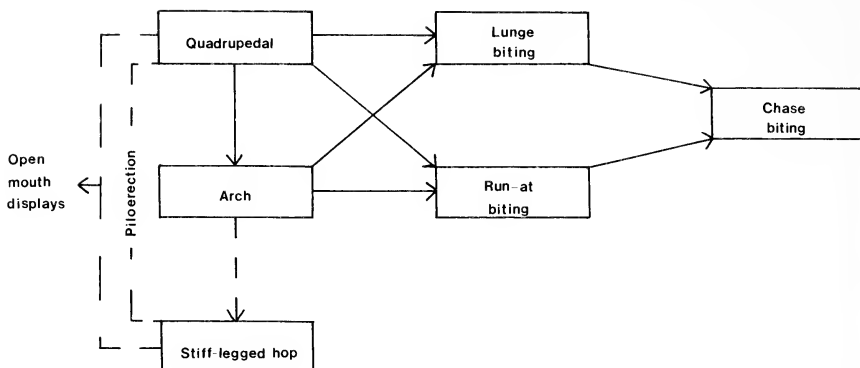


Fig. 5.—Agonistic behavior sequences for *Galea spixii*. Open mouth displays occur in all postures.

ues to move closer. It also denotes a high probability of an aggressive attack when presented by an approaching animal. The hindlegs and thick muscular tail constitute the three points of a triangle, thus maintaining a stable base for balancing in the upright postures.

Full erect.—This posture conveys the same information as semi-erect but at an increased level of intensity. Forepaws are generally raised higher and extended forward slightly.

Locked upright.—Numerous attempts to grasp the opponent's shoulders may be made before both individuals secure a firm grip. Immediately after the grips are secured, the animals begin a vigorous shoving match in which each attempts to push the other onto its side or back. These bouts may go on continuously for several minutes before one animal gains the advantage. As in the simpler semi-erect and full erect postures, no attempt is made to bite the opponent when both are upright, even though their heads are in close proximity during the locked interval. Biting is typically directed at the back or hind-quarters as soon as one animal succeeds in throwing its opponent to the ground.

Strike with forepaws.—Strikes are delivered from both semi-erect and full-erect postures in two general styles. The first is of a limited extent; the animal maintains balance and position and immediately returns to an upright posture. The second is the final movement of a forward lunge in which the animal launches its entire body at the opponent.

Chest kick.—This tactic is typically observed only in conjunction with a locked upright. One individual upsets the balance of the other,

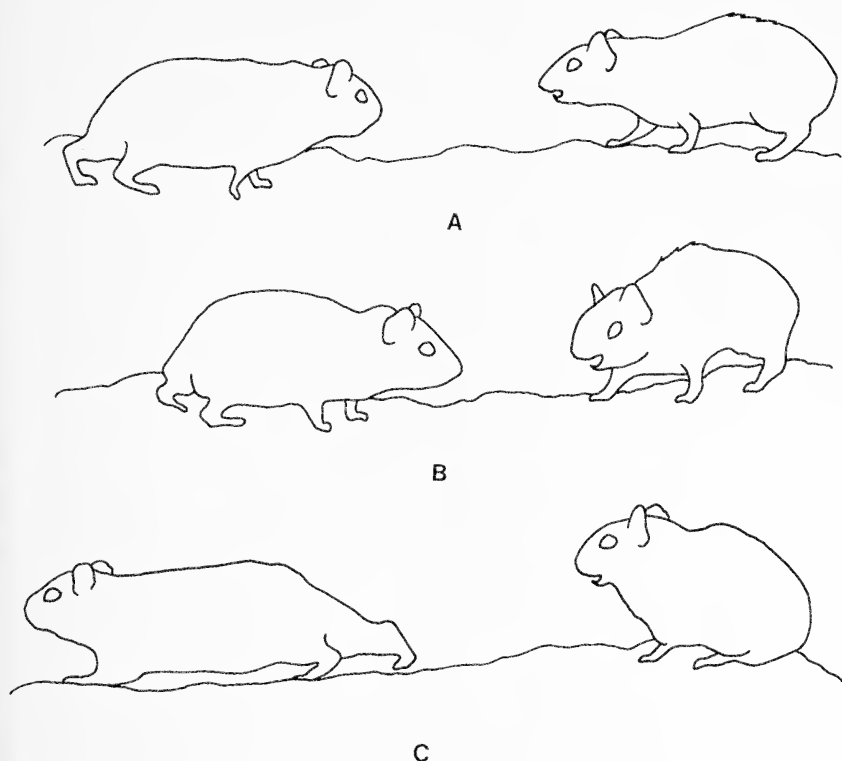


Fig. 6.—Agonistic displays and postures for *Galea spixii*. When being approached, the animal on the right exhibits a defensive open mouth display and piloerection (A). Continued approach evokes the arched posture (B). The intruder turns away, assuming the defensive tail up posture (C).

jumps off the ground, swings its hind legs back, and then kicks them forward and up into the chest of the opponent. Several individuals caught by chest kicks suffered serious damage, such as broken forelegs or ribs.

Wrestle.—Bouts are usually of brief duration. Each individual attempts to obtain a position on the back of the other. Biting is common while wrestling.

Chase.—Active pursuit of a fleeing animal. Biting is generally directed at the hindquarters.

Agonistic behavior was observed in only 21 of 59 trials (Table 5). Upright postures and displays were the predominant components of aggressive behavior.

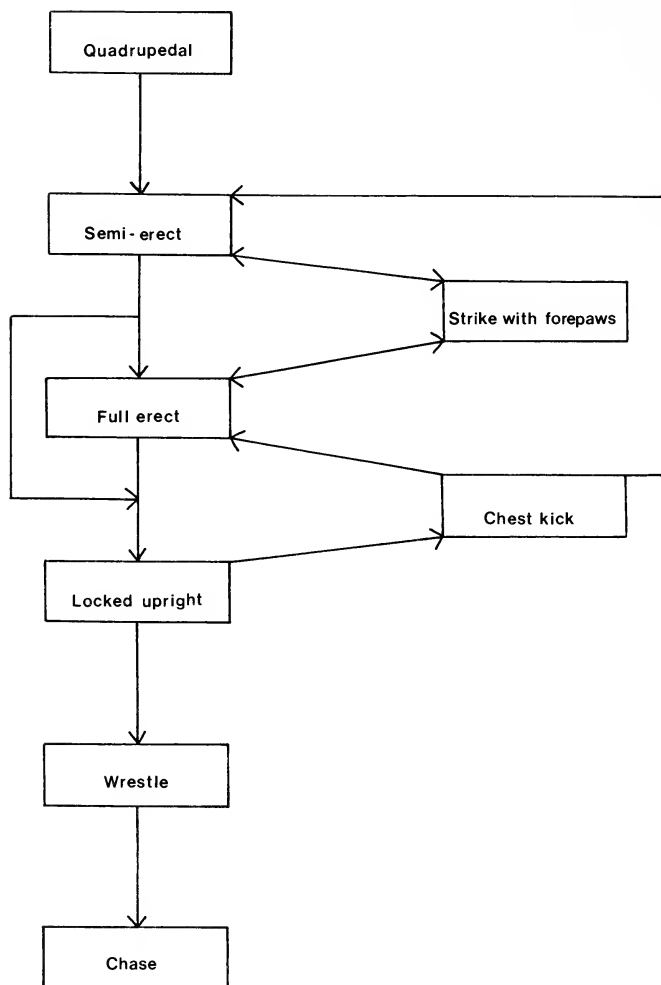


Fig. 7.—Agonistic behavior sequences for *Thrichomys apereoides*.

INTERSPECIFIC AGONISTIC BEHAVIOR

Thrichomys apereoides versus *Bolomys lasiurus*.—Initiation of first approach was similar in both species (Table 6). *Thrichomys apereoides* never engaged in prolonged aggressive behavior toward *B. lasiurus* and essentially ignored the smaller species. Some *Bolomys* actively avoided *Thrichomys*, but mutual interactions were minimal. Agonistic postures in *Bolomys* (Table 7) did not elicit responses from *Thricho-*

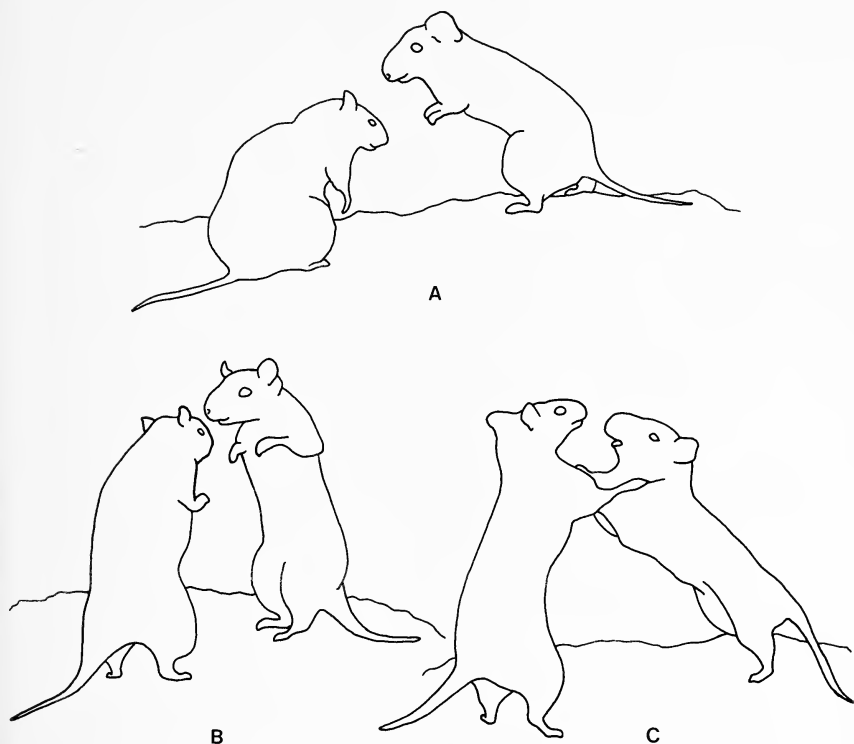


Fig. 8.—Agonistic displays and postures for *Thrichomys apereoides*. Animals mutually assume the semi-erect posture (A), then stretch into the full erect posture. Brief preliminary sparring may occur before the animals enter the locked upright position (C). A vigorous pushing contest ensues.

mys, but persistent approaches sometimes did provoke defensive actions by *Thrichomys*.

Thrichomys apereoides versus *Galea spixii*.—*Galea* initiated the first approach twice as often as *Thrichomys* (Table 6). *Galea* postures and displays did not invoke agonistic responses in *Thrichomys* unless the *Galea* were in close proximity. *Thrichomys* typically reacted with a semi-erect defensive posture and sometimes struck at the face of the *Galea* with their forepaws (Table 7). Dominance was clearly established in only two of the 20 trials; 12 of the trials had no agonistic interactions.

Thrichomys apereoides versus *Kerodon rupestris*.—The much larger species, *K. rupestris*, initiated the first approach in 19 of the trials and the first aggressive approach in seven trials (Table 6). Approaches

Table 6.—*Selected results of interspecific agonistic encounters.*

Genera tested	Initiate first approach	Initiate first aggressive approach	Physical contact with opponent	Flee from opponent one or more times	Clearly dominant	Dominance not established	No aggression
<i>Thrichomys</i>	1	1	10	7	0	13	5
<i>Kerodon</i>	19	7	5	0	2		
<i>Thrichomys</i>	7	1	6	2	1	6	12
<i>Galea</i>	13	5	2	4	1		
<i>Kerodon</i>	15	11	12	0	13	2	5
<i>Galea</i>	5	4	1	14	0		
<i>Thrichomys</i>	9	1	5	0	7	4	9
<i>Bolomys</i>	12	5	2	9	0		

or upright postures by *Kerodon* typically prompted *Thrichomys* into assuming an upright posture (15 trials), often accompanied by a fore-paws strike (nine trials). Most of the encounters were stand-offs (13 of 20). *Kerodon* never fled from *Thrichomys*.

Kerodon rupestris versus *Galea spixii*.—Even though *Galea* initiated the first aggressive approach in four trials, *Galea* were never judged to be dominant (Table 6). *Kerodon* established dominance in 13 of the trials. *Kerodon* made physical contact with *Galea* in 14 trials, generally from a semi- or full erect posture. Approximately one-half of the *Galea* received serious injuries or died as a result of the agonistic encounters with *Kerodon*. Arched postures by *Galea* did not effectively stop approaches by the opponent as they often did in intraspecific encounters.

DISCUSSION

Monodelphis domestica and *Bolomys lasiurus* were very intolerant of conspecifics of either sex. Open mouth threats by *Monodelphis* were generally effective at preventing approaches. *Bolomys*, on the other hand, were more likely to engage in physical contact. Adoption of upright postures was characteristic of the *Bolomys* encounters. Both species react agonistically if the minimum "individual distance" (Hediger, 1941 as cited by Wilson, 1975) is breached. In periods of high density population, the probability of chance encounters between *Bolomys* individuals is escalated but the results of the encounter experiments in neutral arenas indicate the adoption of upright defensive postures frequently fails to inhibit approaching animals. Do *Bolomys* typically engage in physical contests in high density situations? If they do, a great deal of time and energy are expended and the risk of serious injury climbs. One particular behavioral sequence probably assumes

greater importance when populations are dense. Alternate stretching was observed in only 15 of 117 trials in the neutral arenas, but effectively eliminated physical contact; when both individuals have attained maximum stretches, their relative sizes are displayed. An attack pressed upon a larger individual is not likely to succeed as a general rule. Indeed, the smaller individual usually dropped out of the full erect posture and moved away from its opponent.

The importance of the stretching sequence was further clarified by a fortuitous incident. Six *Bolomys* (three males and three females) were transferred to a vacant glass-fronted holding cage as a temporary measure. The individual *B. lasiurus* immediately reacted to movements by other animals with upright postures and defensive strikes. After a flurry of physical contact, the animals began to exclusively utilize the alternate stretching sequence. Several hundred encounters were observed in the first hour; in almost every instance, physical contact was circumvented and the smaller animal was the first to abandon the upright posture. The smallest individual frequently "won" encounters with much larger individuals, however, when it was standing on the ledge around the base of the cage. The additional height of the ledge permitted it to stretch higher than individuals which actually had much larger body sizes. If this behavioral sequence functions in the same fashion in natural situations, it would allow high density populations to exist with a minimum of physical aggression.

Agonistic behavior was observed in 59 of 108 *Galea* trials. Male *Galea*, especially individuals with descended testes, reacted to other *Galea* (including other testes descended males) with sexual interest. Females tended to interact aggressively with other females. Female *Galea* may maintain a core area exclusive of other female core areas, whereas males move about in search of sexually receptive females, interacting aggressively with other males only in the vicinity of estrous females. More field data are needed to substantiate this hypothesis.

The incidence of agonistic behavior was lowest in *Thrichomys*, occurring in only 21 of 59 trials. This was unexpected in view of the fact that female home ranges overlapped very little with other female home ranges, whereas male home ranges overlapped those of the females, but are relatively exclusive of other male home ranges. Avoidance rather than active defense was the general rule. Two pregnant females with neighboring home ranges were removed from the grid after the population study was terminated and subsequently paired in the neutral arena. A mutual approach and nose-to-nose contact immediately progressed into a "ritualistic" locked-upright encounter. Perhaps under natural conditions, violent encounters only occur at initial meetings, whereas subsequent avoidance results in exclusive home ranges.

In the *Kerodon rupestris* versus *Galea spixii* interspecific encoun-

ters, *Kerodon* was clearly dominant. *Galea*'s displays and postures were all of a quadrupedal nature. *Kerodon* used upright postures to strike down at the *Galea*, often dropping from the full erect onto the back of the *Galea*, pinning them to the ground with the forelegs; biting was then directed at the base of the skull and neck. This posture was essentially the same as the *Kerodon* mating posture. The upright postures which were successful tactics when *Kerodon* was paired with *Galea* were largely ineffectual against *Thrichomys*. Individual *Thrichomys* would typically give way before the much larger *Kerodon*, but if backed into a corner they would maintain an upright posture for extended periods and readily resorted to defensive strikes. The upright postures of *Thrichomys* gave them an advantage over *Galea* similar to that possessed by *Kerodon*, but the *Thrichomys* were not actively aggressive, reacting only when *Galea* individuals approached too closely. Both *Thrichomys* and *Bolomys* extensively used upright postures in intraspecific encounters, but *Thrichomys* generally ignored the much smaller *Bolomys*.

Some of the expected results were observed. *Thrichomys* interacted very little with *Bolomys* and *Galea* unless approached too closely, in which case they assumed upright postures and were likely to strike at the intruder. *Kerodon* was aggressive toward and dominant over *Galea* but was unexpectedly aggressive toward *Thrichomys*.

The existence of active aggression by *Kerodon* toward *Galea* and *Thrichomys* further clarifies the distributional patterns observed on the grid. *Kerodon* and *Thrichomys* occupy the same habitat but they have opposite activity patterns; *Kerodon* is largely diurnal and *Thrichomys* is nocturnal with crepuscular peaks. Coexistence through temporal separation is thus possible. *Galea*, however, are diurnal and likely to encounter *Kerodon*. The complex three-dimensional structural diversity of the rock habitats prevents *Kerodon* from totally excluding *Galea*, but the level of interaction is sufficient to reduce the density of individuals. Partial exclusion of *Galea* by *Kerodon* explains why *Galea* is the only non-murid not concentrated in the more favorable rock habitats during the dry months. The presence of *Kerodon* in a particular site may serve as a continuous, passive deterrent to future encroachment by individual *Galea* that have experienced agonistic responses from the much larger *Kerodon*. Hypothetically then, *Galea* would be expected to exhibit a greater degree of utilization of rock habitats when *Kerodon* is absent. Lacher (1981) mixed various combinations of *Kerodon* and *Galea* colonies under semi-natural conditions and consistently found that *Kerodon* were dominant over *Galea* and forcibly excluded them from the simulated rocky microhabitat. The aggressive nature of *Kerodon* might be related to the distribution of free water in the rocks. Restricting the access of other species to

the temporary, limited sources of water through a behavioral response might be of great significance because *Kerodon* has weakly-developed water conservation capabilities (Streilein, 1982b).

OVERVIEW

Environmental unpredictability has been the predominant characteristic of the Caatinga in both evolutionary and ecological time (Streilein, 1982a). Wet-dry climatic cycles in the Quaternary induced concomitant, large-scale contractions and expansions of the Caatinga. Extended periods of extreme drought continue to punctuate the "normal" semiarid state at irregular intervals. The adaptation of the small mammal fauna to the fluctuating Caatinga environment has been dependent upon the presence of a large number of granitic outcroppings; the outcroppings apparently served as relatively stable, mesic "micro-refugia" during the dry phases of the climatic cycle and moderate the generally xeric ambient conditions and intermittent occurrence of severe environmental stress over ecological time.

The small mammal fauna of the Caatinga did not exhibit an advanced degree of physiological adaptation for aridity. Two species, *Thrichomys apereoides* and *Monodelphis domestica*, had moderate water conservation capabilities, but the other species examined had very poorly developed capabilities in comparison to small mammal species in other xeric regions (Streilein, 1982b). Some species of caviomorphs and marsupials—*Thrichomys apereoides*, *Kerodon rupestris*, *Monodelphis domestica*, and *Didelphis albiventris*—have compensated for the deficiency in physiological mechanisms with a behavioral response, selecting the relatively mesic granitic habitat types (Streilein, 1982d). None of the murid rodents exhibited this behavior.

In a fluctuating environment, the timing of reproduction is critical. The large amount of energy expended in the production of young will be lost unless individuals can accurately track environmental conditions, reproducing only during intervals of favorable conditions. Two general strategies that could have evolved in the Caatinga to minimize energy loss in reproduction are: 1) consistently concentrate reproductive effort in the interval when favorable conditions are most probable; 2) retain reproductive flexibility in order to rapidly respond to ephemeral, favorable conditions (Streilein, 1982c). *Didelphis albiventris* was the only Caatinga species that exhibited synchronized reproduction; timing the breeding season such that the young are weaned in the months when water surpluses are most probable. Reproductive patterns in the five murid species and *Galea spixii* did not parallel either strategy. Parturition occurred year round, even during periods of pronounced water stress, and essentially all of the mature females in the populations were reproductively active. A third strategy is also feasible

in the Caatinga because microrefugia are readily available. Three species, *K. rupestris*, *T. apereoides*, and *M. domestica*, were thus able to circumvent the general environmental constraints by preferentially utilizing the granitic outcroppings; reproduction occurred throughout the year, but generally at a lower rate and with a smaller gross output of young.

Intense reproductive effort in the murid rodents was not reflected in increased population size or in age structure (Streilein, 1982c). None of the murids were able to consistently maintain elevated population levels in the Caatinga even though the same species were the most abundant small mammals in the Cerrado biome. Populations were mainly composed of adults, indicating a very high level of mortality in young individuals. The marsupials and caviomorph rodents that inhabited the granitic outcroppings were able to maintain higher population levels than the murids. The only caviomorph that did not preferentially utilize the rocky habitats, *Galea spixii*, exhibited a reproductive effort that was more similar to the murid characteristics than to those of the other caviomorphs.

Several factors illustrate the generally low level of adaptation to the Caatinga in the murid rodents. First, four of the five murid species—*Bolomys lasiurus*, *Calomys callosus*, *Oryzomys eliurus*, and *O. subflavus*—were found only in the immediate vicinity of the Chapada do Araripe, an extension of the Cerrado biome that stretches unbroken through nearly three-fourths of the width of the Caatinga; most of the caviomorphs and marsupials had widespread geographic distributions within the Caatinga. Second, the habitats occupied in the Caatinga were likely to experience severe water stress, but the murids were not physiologically well-adapted for aridity. Third, low population levels were typical in the few habitats occupied; however, the Caatinga habitats closely corresponded with habitats that supported dense populations in the Cerrado. Fourth, none of the murids utilized the granitic outcroppings, the most mesic, stable habitats available in the Caatinga.

The murids probably invaded the Caatinga through the Cerrado, and thus did not possess suitable preadaptations for the xeric, unpredictable environment of the Caatinga. Granitic outcroppings are extremely rare in the Cerrado, so these species could not develop an affinity for the most advantageous habitat available in the Caatinga. The Cerrado is also much more predictable and mesic (due in part to a more favorable geological composition) compared to the Caatinga. Most of the murids are caught in a situation wherein the habitat types in which they were previously successful are irregularly subjected to prolonged drought. Alternately, they also experience extended intervals of heavy precipitation. The widely divergent selection pressures that accompany these disparate climatic phenomena may effectively prevent ac-

cumulation of specialization for the "mean" semiarid state. *Wiedomys pyrrhorhinos*, however, has a broad geographic distribution in the Caatinga and is also the only small mammal species that is found solely in the most extensive habitat type available, the low thorn scrub formations. This preference for thorn scrub suggests that *Wiedomys* is evolving into a "true" thorn scrub specialist, at least within the limits imposed by the climatic vagaries. The other murid species may simply not have had an adequate period of time for adaptation.

The primary feature of the well-adapted species is the pronounced affinity for the microrefugia that exist within the Caatinga, at least during intervals of water stress. The evolution of this behavioral response resulted in a decreased emphasis on physiological adaptations to aridity. None of the common caviomorphs or marsupials exhibited preference for the thorn scrub habitats. *Galea spixii* utilized the outcroppings to a lesser extent than the other species, but was subordinate to *Kerodon rupestris* in agonistic interactions and was apparently partially excluded from the outcroppings.

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NOTES ON THE DIATOM GENUS *BERGONIA* TEMPÈRE, INCLUDING THE DESCRIPTION OF A NEW SPECIES

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ABSTRACT

The extinct marine diatom genus *Bergonia* Tempère is known only from Eocene sediments. A new species described in this paper, *Bergonia angelica*, is intermediate in evolutionary development between the two previously known species in the genus—*Bergonia primitiva* and *Bergonia barbadensis*. The distinctive morphologies of the three species of *Bergonia* and their evolutionary progression have potential as valuable biostratigraphic tools.

INTRODUCTION

Bergonia Tempère (1891), an extinct genus of the diatom family Asterolampraceae H. L. Smith (1872), consists of three species—*Bergonia barbadensis* Tempère (1891), *Bergonia primitiva* Gombos (1980), and *Bergonia angelica* Gombos, new species. The known geologic range of the genus is from late Early Eocene to Late Eocene. The known geographic distribution of the genus is from about 40°N latitude to about 50°S latitude (author's notes). All species of the genus are presumed to have been planktonic and marine in habitat because of their occurrence only in pelagic marine sediments.

Two species of *Bergonia* have previously been described—*Bergonia barbadensis* Tempère (1891) and *Bergonia primitiva* Gombos (1980). A third species, *Bergonia angelica*, is described herein and represents a form intermediate in development between *Bergonia primitiva* and

¹ Address: Exxon Production Research Company, P.O. Box 2189, Houston, TX 77001. Submitted 8 February 1982.

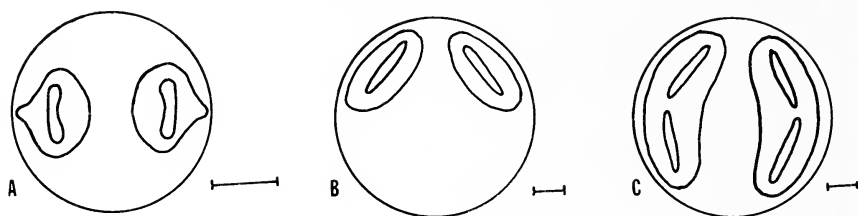


Fig. 1.—Diagrammatic representations of the arrangements of rays and ray-slits in the three known species of *Bergonia*. (A) *Bergonia primitiva*, (B) *Bergonia angelica*, (C) *Bergonia barbadensis*. Scales equal 10 micrometers.

Bergonia barbadensis, which are, respectively, the oldest and youngest species in the genus.

The unifying characteristic of the species of *Bergonia* is the tangential orientation of the ray-slits, as opposed to the radial orientation of ray-slits, typical in all other genera of the Asterolampraceae (Gombos, 1980). Other characteristics of *Bergonia* include the presence of two subovate to reniform rays which are near-marginal in position and exhibit little, or no, marginal prolongation. The various arrangements of rays and ray-slits in the three species of *Bergonia* are illustrated diagrammatically in Fig. 1.

TAXONOMY

Class Bacillariophyceae

Order Centrales

Suborder Coscinodiscineae

Family Asterolampraceae H. L. Smith 1872

Genus *Bergonia* Tempère 1891

***Bergonia angelica*, new species**

Fig. 2C

Description.—Valves circular, flat to very slightly arched. Valve surface areolate with two tangentially elongated, reniform rays situated adjacent to each other or slightly separated in one half of the valve face; rays oriented at an angle of 83° to each other in the holotype; ray-slits elongate, tangentially oriented. Areolae arranged in slightly curved fascies; areolae larger in valve center, decreasing in size toward valve margin; 6 to 7 areolae in 10 micrometers along rows; margin with 2 or 3 rows of pores. A single labiate process is located, near the margin, close to the tip of each ray-slit (Fig. 3). Diameter of holotype is 65 micrometers; long axis of ray is 38 micrometers; minor axis of ray is 16 micrometers; length of ray-slit is 27 micrometers; width of ray-slit is 5 micrometers.

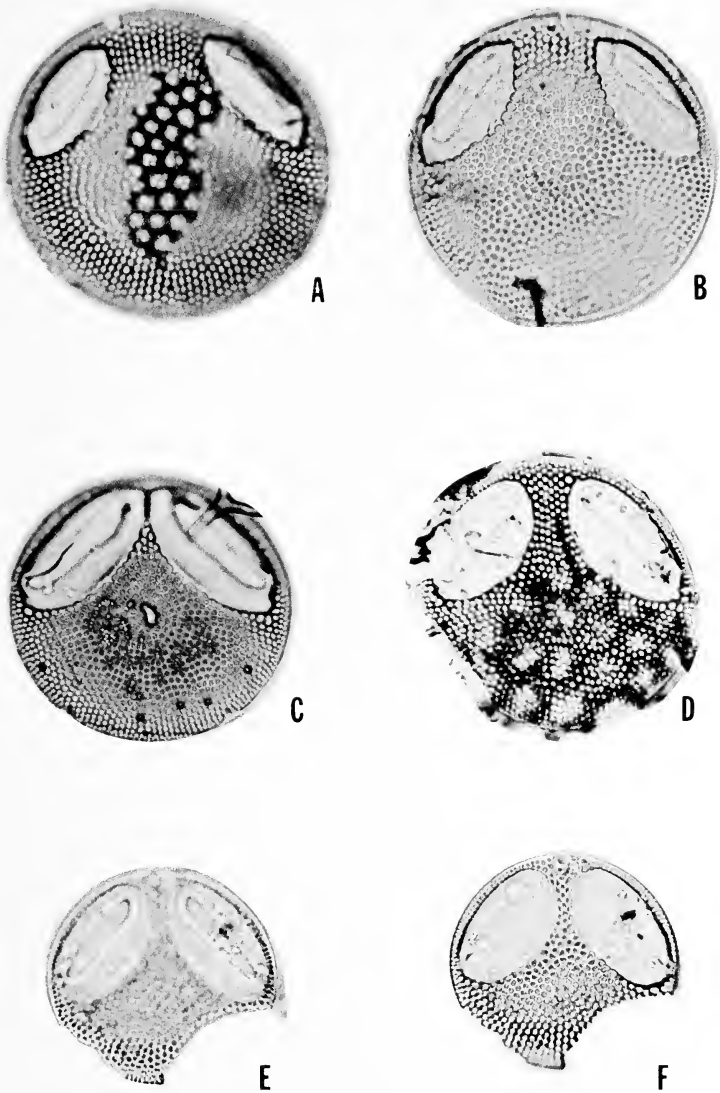


Fig. 2.—Photomicrographs of *Bergonia angelica*, new species. All magnifications $\times 500$. (A) DSDP 512-11-3, 60–62 cm; (B) DSDP 512-11-1, 78–80 cm; (C) Holotype, DSDP 512-11-3, 60–62 cm; (D) DSDP 206C-17-4, 120–122 cm; (E & F) *Islas Orcadas* piston core 1678-44, 0–1 cm.

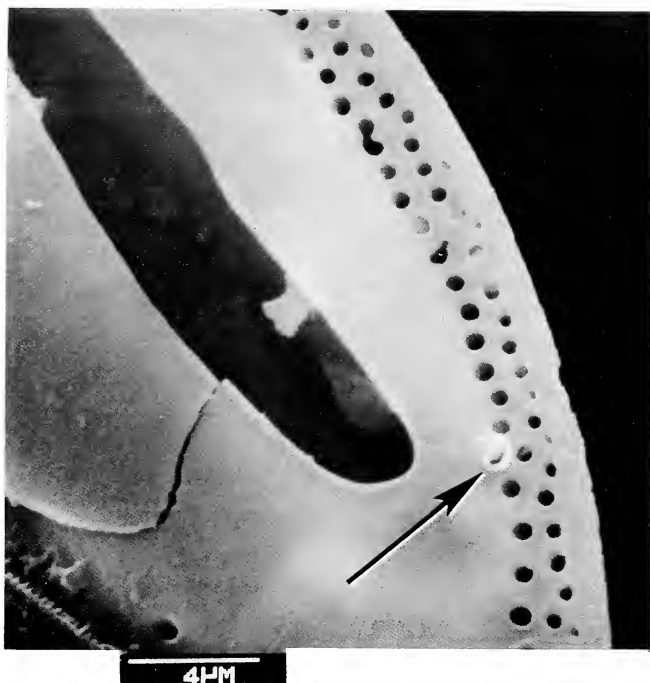


Fig. 3.—Scanning electron photomicrograph of the internal view of the ray and ray-slit of *Bergonia angelica*, new species, showing broken labiate process (indicated by arrow). Specimen from DSDP 512-11-1, 78–80 cm.

Holotype.—Exxon Production Research Company slide preparation D283U3; specimen is marked on cover slip and is illustrated herein as Fig. 2C.

Repository.—Carnegie Museum of Natural History, Section of Invertebrate Fossils, Pittsburgh, Pennsylvania. Catalogue number 34389.

Type locality.—Deep Sea Drilling Project Site 512 (lat. 49°52.194'S; long. 40°50.713'W) located on the Maurice Ewing Bank at the eastern extremity of the Falkland (Malvinas) Plateau.

Type strata.—DSDP Hole 512, Core 11, Section 3, Interval 60–62 cm, or 41.9 to 41.11 meters below the sediment surface.

Age.—Middle Eocene.

Other occurrences.—DSDP Hole 206C (lat. 32°00.75'S; long. 165°27.15'E), Core 17, Sections 1 through 4. Located on the Lord Howe Rise between Australia and New Zealand. ARA (Armada Republica Argentina) ISLAS ORCADAS piston core 1678-44 (lat. 49°58.7'S; 42°38.4'W), 1 cm below the sediment surface. Located on

the Maurice Ewing Bank at the eastern extremity of the Falkland (Malvinas) Plateau.

DISCUSSION

At present, *Bergonia primitiva* (Fig. 1A) is known only from the late Early Eocene (Gombos, 1980). This species is rather small and has two oppositely aligned subovate rays with tangentially oriented ray-slits. *Bergonia primitiva* is the oldest known species of the genus (Gombos, 1980). Therefore, it represents the most primitive evolutionary stage of the genus. The small size of the valves and the oppositely aligned, subovate rays of *Bergonia primitiva* distinguish it from the other species of the genus and are assumed to represent primitive characteristics.

Begonia angelica (Fig. 1B) is, at present, known only from Middle Eocene sediments. The valves of *Bergonia angelica* are larger than those of *Bergonia primitiva*. The rays are reniform in shape and occupy a considerable portion of the valve face, though not as great an area as is occupied by the rays of *Bergonia barbadensis*. The rays of *Bergonia angelica* are migrated to one half of the valve face. The ends of the rays abut against each other or are separated by a few microns. Each ray of *Bergonia angelica* possesses a single, tangentially aligned ray-slit.

Bergonia barbadensis (Fig. 1C) is known from Middle Eocene to Late Eocene sediments (Gombos, 1980). *Bergonia barbadensis* is characterized by large valves with two very large reniform rays which frequently occupy more than half the valve face. The rays are not aligned directly opposite each other, but are slightly migrated toward one half of the valve face. The ray-slits of *Bergonia barbadensis* are unique in that they are divided in their middle portion by a hyaline bridge. *Bergonia barbadensis* is the youngest species of the genus and therefore represents the maximum evolutionary development of the genus.

When present in sediment, the various species of *Bergonia* are quite valuable in determining the age of the sediment. The geological occurrences of the three species are discussed above. At present, relatively few Paleogene diatomaceous sections have been reported on in the literature. It is very likely that as more biostratigraphic studies of the older diatoms are conducted, the stratigraphic ranges of the three species will be more precisely determined.

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THE BAT FAUNA OF JABAL AL AKHDAR, NORTHEAST LIBYA

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ABSTRACT

Fifty nine specimens of bats representing eight species in three families are reported from the region of Jabal Al Akhdar in northeastern Libya. *Nyctalus lasiopterus* is reported for the first time from Africa, while *Pipistrellus pipistrellus*, *Miniopterus schreibersii* and *Tadarida teniotis* are new additions to the fauna of Libya. *Rhinolophus clivosus*, *R. mehelyi*, *Pipistrellus kuhlii*, and *Plecotus austriacus* are additional distributional records from Libya. Taxonomic comments are given. Although distinctive, the bat fauna of Jabal Al Akhdar is considered of Mediterranean origin and includes taxa seemingly closely associated with those from southcentral Europe rather than the Eastern Mediterranean and Maghreb regions.

INTRODUCTION

There are few reports on the bat fauna of Libya (De Beaux, 1932, 1938; Festa, 1921; Hufnagel, 1972; Klaptocz, 1909; Setzer, 1957; Toschi, 1954; Zavattari, 1934). Almost no collecting of bats has been done in the Jabal Al Akhdar (=the green mountain) in northeastern Libya (previously referred to as "Cyrenaica" or the Cyrenaica Plateau). The Jabal Al Akhdar region is characterized by a Mediterranean Maquis type vegetation (Zohary, 1973) and is unique in this part of northern Africa.

Through the courtesy of the Kuf National Park administration in

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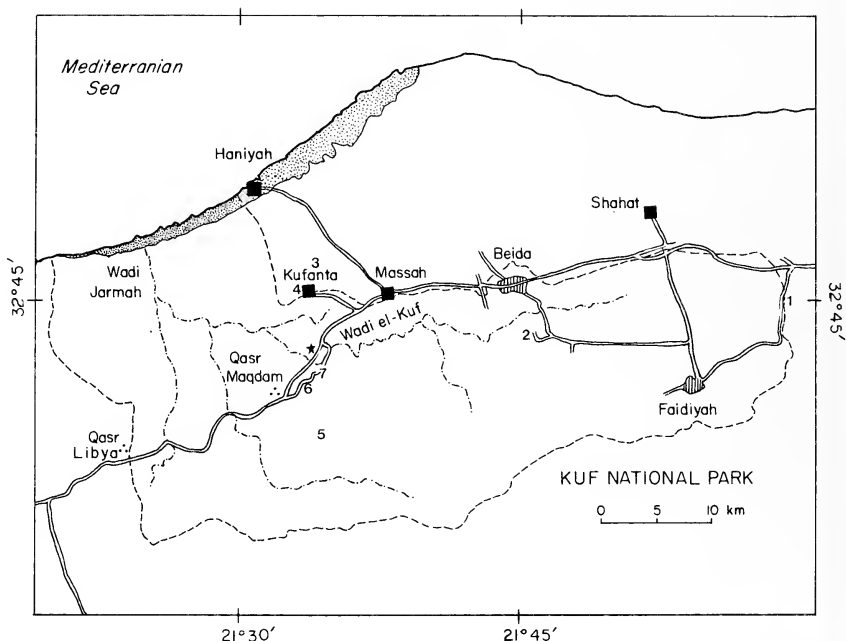


Fig. 1.—Map of the Kuf National Park and environs of Jabal Al Akhdar illustrating collecting localities mentioned in the text (numerals).

Libya, an inventory of small mammals, especially bats, was made in the park from 8 March through 9 April 1981. During that interval, 58 specimens of bats, representing eight species in three families, were collected. Many of these specimens represent taxonomically and zoogeographically important records for this region of Africa and are reported in this paper.

MATERIALS AND METHODS

The collecting localities mentioned in the accounts of species and their coordinates are listed below (numbers correspond to Fig. 1):

- 1) Al Abraq, 5 km SW—32°45'N, 21°58'E.
- 2) Baida, 4 km S—32°44'N, 21°43'E.
- 3) Haniya, 8 km SSE—32°46'N, 21°27'E.
- 4) Kufanta—32°46'N, 21°34'E.
- 5) Qasr Maqdam, Ruins 6 km SE—32°38'N, 21°36'E.
- 6) Wadi Al Kuf, unnamed cave—32°41'N, 21°33'E.
- 7) Wadi Al Kuf, mistnetting site—32°42'N, 21°35'E.

Unless otherwise indicated in the specimens examined, all specimens were prepared as conventional museum specimen skins and skulls and were collected by the senior



Fig. 2.—Mistnetting site at edge of water pool in Wadi Al Kuf. Habitat of *Pipistrellus kuhlii*, *P. pipistrellus*, *Nyctalus lasiopterus*, *Plecotus austriacus*, and *Tadarida teniotis*.

author in 1981. In some instances, the field numbers, indicated by the prefix MQ, are given for specimens not yet catalogued. Specimens will be divided with most deposited in Carnegie Museum of Natural History, Pittsburgh, and some will be deposited in the Kuf National Park Museum, Beida, Libya. One specimen of *Pipistrellus pipistrellus* from 5 km SW of Al Abraha was examined in the National Museum of Natural History, Washington (USNM). External measurements were taken from the field tags and forearm and cranial measurements were taken with dial calipers. All measurements are given in millimeters. Selected external and cranial measurements of the eight species are given in Tables 1 and 2.

In the species accounts, families and genera are listed as they appear in Corbet (1978) but the species are listed alphabetically.

JABAL AL AKHDAR

The Jabal Al Akhdar is a mountainous region of northeastern Libya, mainly south of the city of Beida. The Wadi Al Kuf, with its tributaries Wadi Beit Saleh and Wadi Sudan, provides the main watershed of the Jabal Al Akhdar (Figs. 1, 2). The watershed consists of wadis cut through the limestone rock, forming many high and narrow valleys. Some valleys are 200 m in depth. Numerous karstic caves and cracks of different sizes occur in the region. Altitude ranges from sea level to 878 m.

Table 1.—External measurements of samples of eight species of bats from Jabal Al Akhdar and some comparative material. Means and ranges of measurements enclosed in parentheses are given for some samples.

Locality, sample, and sex	Total length	Length of tail	Length of hindfoot	Length of ear	Length of forearm
<i>Rhinolophus clivus</i>					
6 km SE Oasr Maqdam (♂)	76	29	10.5	19	50
Roman aqueduct, Kufanta (♂)	78, 76	26, 30	10, 10	18, 21	47, 49
<i>Rhinolophus mehelyi</i>					
Wadi Al Kuf (6 ♂♂)	72.5 (70–77)	24.2 (22–26)	9.8 (8.5–11)	20.0 (19–21.5)	47.3 (46–48)
Wadi Al Kuf (4 ♀♀)	72.8 (70–75)	26.3 (22–29)	9.8 (8–11)	20.4 (19–21)	47.3 (46–49)
<i>Pipistrellus kuhlii</i>					
Wadi Al Kuf (2 ♂♂)	81, 85	38, 41	7, 7	13, 12.5	34, 34
<i>Pipistrellus pipistrellus</i>					
Wadi Al Kuf (10 ♂♂)	71.6 (67–78)	31.2 (28–33)	6.1 (4–8)	10.2 (8–11)	31.2 (30–32)
Wadi Al Kuf (6 ♀♀)	74.5 (71–82)	32.0 (30–34)	6.5 (6–7)	10.4 (10–11)	31.5 (29.7–32.5)
<i>Nyctalus lasiopterus</i>					
Wadi Al Kuf (2 ♂♂)	143, 150	53, 53	14.5, 13	21, 22	62.5, 61
Wadi Al Kuf (4 ♀♀)	144.5 (138–152)	56.3 (48–62)	14.4 (12.5–16)	20.8 (19–23)	61.3 (59–64)
<i>Plecotus austriacus</i>					
Wadi Al Kuf (♀)	98	42	9	36	40
6 km SE Qasr Maqdam (♂)	95	45	8.5	34.5	38

Table 1.—Continued.

Locality, sample, and sex	Total length	Length of tail	Length of hindfoot	Length of ear	Length of forearm
Egypt: Dandara Temple (2 ♀ ♀)	95, 93	48, 46	8, 8.5	38, 35	38.5, 39
Egypt: Dandara Temple (1 ♂)	96	45	8	37	37
<i>Miniopterus schreibersii</i>					
Wadi Al Kuf (3 ♀ ♀)	107.7 (106–111)	49.3 (48–50)	8.8 (8.5–9)	8.3 (8–8.5)	43.5 (43–44)
<i>Tadarida teniotis</i>					
Wadi Al Kuf (8 ♂ ♂)	126.3 (119–132)	41.4 (37–48)	11.4 (10–12.5)	29.5 (25–31)	58.9 (56–61)
Wadi Al Kuf (4 ♀ ♀)	130.8 (120–136)	46.8 (46–48)	11.9 (11.2–12.3)	29.3 (26–31)	61.0 (59–63)

Table 2.—Selected cranial measurements of specimens listed in Table 1. Means and ranges of measurements as in Table 1.

Locality, sample, and sex	Greatest length of the skull	Zygomatic breadth	Length of maxillary tooththrow	Length of mandible	Length of mandibular tooththrow
<i>Rhinolophus clivosus</i>					
6 km SE Qasr Maqdam (♂)	20.6	11.1	7.6	13.4	8.6
Roman aqueduct, Kufanta (♂, ♀)	20.3, 20.4	10.9, 11.0	7.5, 7.5	13.2, 13.2	8.2, 8.1
<i>Rhinolophus mehelyi</i>					
Wadi Al Kuf (6 ♂♂)	19.5 (19.3–19.8)	10.2 (9.9–10.6)	6.8 (6.7–6.9)	12.0 (11.9–12.1)	7.5 (7.4–7.7)
Wadi Al Kuf (4 ♀♀)	19.5 (19.4–19.5)	10.4 (10.2–10.5)	6.7 (6.6–6.8)	12.0 (11.9–12.1)	7.5 (7.3–7.7)
<i>Pipistrellus kuhlii</i>					
Wadi Al Kuf (2 ♂♂)	13.4, 13.8	8.4, 9.0	4.7, 4.9	9.4, 9.3	5.3, 5.5
<i>Pipistrellus pipistrellus</i>					
Wadi Al Kuf (10 ♂♂)	12.5 (12.2–12.7)	7.6 (7.4–7.9)	4.3 (4.2–4.4)	8.2 (8.0–8.4)	4.7 (4.5–4.8)
Wadi Al Kuf (6 ♀♀)	12.4 (11.5–12.7)	7.7 (7.0–8.0)	4.3 (4.0–4.4)	8.1 (7.4–8.5)	4.7 (4.4–5.0)
<i>Nyctalus lasiopterus</i>					
Wadi Al Kuf (2 ♂♂)	22.7, 22.1	15.7, 15.4	9.0, 8.6	16.8, 16.3	9.7, 9.4
Wadi Al Kuf (4 ♀♀)	22.4 (22.2–22.7)	15.5 (15.1–16.0)	8.8 (8.7–8.9)	16.5 (16.3–16.7)	9.5 (9.4–9.7)
<i>Plecotus austriacus</i>					
Wadi Al Kuf (♀)	17.7	9.0	5.7	11.0	6.5
6 km SE Qasr Maqdam (♂)	17.6	9.1	5.2	10.6	6.2
Egypt: Dandara Temple (2 ♀♀)	16.8, 16.8	8.5, 8.6	5.3, 5.4	9.9, 10.1	5.5, 5.9
Egypt: Dandara Temple (1 ♂)	17.0	8.6	5.5	10.1	6.1

Table 2.—Continued.

Locality, sample, and sex	Greatest length of the skull	Zygomatic breadth	Length of maxillary toothrow	Length of mandible	Length of mandibular toothrow
<i>Miniopterus schreibersii</i>					
Wadi Al Kuf (2 ♀ ♀)	14.7, 14.8	8.1, 8.2	5.6, 5.7	10.0, 10.4	6.4, 6.5
<i>Tadarida teniois</i>					
Wadi Al Kuf (8 ♂ ♂)	23.9 (23.3–24.8)	14.0 (13.5–15.1)	8.7 (8.5–9.0)	16.3 (15.8–17.0)	9.8 (9.6–10.2)
Wadi Al Kuf (4 ♀ ♀)	23.5 (23.2–23.8)	13.4 (13.1–13.7)	8.6 (8.5–8.6)	16.3 (15.9–16.7)	9.7 (9.5–9.8)

The climate of the area is mild Mediterranean. The rainfall ranges between 300 and 600 mm per year, with most of the precipitation occurring during the winter months of November through February. Temperatures range from highs of 35°C in July and August to below freezing during January. Fog occurs extensively during winter months.

The vegetation of the Jabal Al Akhdar is a Maquis type. Groves of *Cupressus sempervirans* occur in protected areas but the main tree species are *Juniperus phoenicea*, *Pistacia lentiscus*, *Arbutus pavarii*, *Cistus salviaefolius*, *Ceratonia siliqua*, *Zizyphus lotus*, *Spartium funceum*, *Olea europea*, *Myrtus communis* and *Quercus coccifera*.

ACCOUNT OF SPECIES

Family Rhinolophidae

Rhinolophus clivosus Cretzschmar, 1828

Specimens examined (5).—Roman aquaduct, Kufanta (2 ♂♂, 1 ♀ in alcohol); Ruins, 6 km SE Qasr Maqdam (1 ♂, 1 ♂ in alcohol).

Remarks.—*Rhinolophus clivosus* was previously recorded from Fezzan by Toschi (1954) as *R. c. schwarzi* Heim de Balsac, originally described from the Algerian Sahara. Hayman and Hill (1971:23) list Algerian Sahara and Libya as the range of *R. c. schwarzi*. The specimens from Jabal Al Akhdar are larger than those examined from the Algerian Sahara (*R. c. schwarzi*) and Egypt (*R. c. brachygnathus*).

The female was not pregnant and the adult males showed no enlarged testes.

Rhinolophus mehelyi Matschi, 1901

Specimens examined.—Unnamed cave in Wadi Al Kuf (6 ♂♂, 4 ♀♀).

Remarks.—*Rhinolophus mehelyi* was listed from "Cyrenaica" by Corbet (1978) based on specimens in the British Museum. The taper of the lancet in our specimens is abrupt and the connecting process of the sella is short and slightly blunt. These characters and the relatively large cranial measurements (Table 2) clearly refer the Jabal Al Akhdar specimens to *Rhinolophus mehelyi* rather than *R. euryale*. However, specimens of the former species originating from eastern Libya and Egypt are small in many cranial and external measurements when compared to those of the Eastern Mediterranean region and northwestern Africa (Algeria, Morocco, Tunisia). This difference may help explain why various authors have identified some Egyptian material as *R. euryale* (see DeBlase, 1972, for a review of this species group in Egypt and Southwest Asia).

The range of measurements of testes of five of the adult males collected was 2.0 to 2.1 in length and 1.0 to 1.6 in width.

Family Vespertilionidae
Pipistrellus kuhlii (Natterer, 1817)

Specimens examined (2).—Wadi Al Kuf, mistnetting site (2 ♂♂).

Remarks.—While *Pipistrellus kuhlii* is common in most of the southwestern Palearctic, including Libya and southwestern Asia (De Beaux, 1932, 1938; Harrison, 1964), it seems to be less common in forested areas where it is outnumbered by the smaller species *Pipistrellus pipistrellus*. This was the case in Jabal Al Akhdar where only two specimens of *P. kuhlii* were caught compared to 18 of *P. pipistrellus*.

The Jabal Al Akhdar specimens are referred to the nominate subspecies. They are indistinguishable in size from specimens of *P. kuhlii kuhlii* from northwestern Africa and southern Europe; measurements of specimens from Crete given by Pohle (1953) agree with those of the Jabal Al Akhdar specimens.

An adult male collected on 9 April had testes measuring 3.5 by 2.0.

Pipistrellus pipistrellus (Schreber, 1774)

Specimens examined (19).—Wadi Al Kuf (8 ♂♂, 3 ♀♀; 2 ♂♂, 2 ♀♀ in alcohol); 4 km S Beida (2 ♂♂); 8 km SSE Haniya (1 ♀); 5 km SW Al Abraha (1 ♂, USNM).

Remarks.—These are the first specimens of *Pipistrellus pipistrellus* reported from Libya. The species is known to occur in the Maghreb, the Eastern Mediterranean region, and in southern Europe (Atallah, 1977; Corbet, 1978; and Harrison, 1964). There seems to be little geographic variation in this species in this part of its continuous range. The populations around the Mediterranean are tentatively all considered to belong to the nominate subspecies.

The range of measurements of testes of seven adult males collected was 1.5 to 3.5 in length and 1.2 to 2.5 in width.

Nyctalus lasiopterus (Schreber, 1780)

Specimens examined (6).—Wadi Al Kuf (2 ♂♂, 4 ♀♀).

Remarks.—These are the first records of *Nyctalus lasiopterus* from Africa, although *Nyctalus noctula* had been reported from Rabat, Morocco (Laurent, 1937), Algiers, Algeria (Dobson, 1878:213; specimen examined in B.M.), and as far south as Lebanon (Lewis and Harrison, 1962) and Oman (Harrison and Jennings, 1980) in southwestern Asia. Another record of *Nyctalus noctula* exists from Mozambique (Peters, 1852). This record was doubted, but in view of the widespread records of the genus in Africa and southwestern Asia and the long migrations known for *N. noctula* in Europe (Roer, 1960), individuals of this genus should be expected elsewhere in northern and eastern Africa.



Fig. 3.—Lateral view of head of a male specimen of *Nyctalus lasiopterus* from Wadi Al Kuf to illustrate ear pinna and tragus shape. Drawn from Kodachrome slide of live specimen.

The cranial measurements of the Libyan specimens are slightly smaller than those of European specimens of *N. lasiopterus*. The external measurements of the Libyan specimens are smaller than are those of European specimens and correspond more closely with those of *N. aviator* (= *N. lasiopterus aviator*) of the Far East. The shape of the ear (Fig. 3) also indicates that the Libyan specimens are referable to *N. lasiopterus*, being thicker and wider at the base than those of *N. noctula*.

The baculum of *N. lasiopterus* closely resembles that of *N. noctula* in shape but is significantly larger in size (Lanza, 1959). The os penes of the two male specimens from Libya measured 7.7 and 8.1 mm in length and 1.15 and 1.18 mm in width at the proximal end. The corresponding measurements for *N. noctula* given by Topal (1958) were 5.51 and 6.22 (mean 5.83) in length and 0.84 to 1.09 (mean 0.94) in width.

An adult male collected on 15 March had testes measuring 2.1 by 1.8.

Six individuals of this species were taken in mist nets in Wadi Al Kuf (Fig. 2). Three females and a single male were netted on 15 March and a single female and male were taken on 28 March and 29 March, respectively.

Plecotus austriacus (Fischer, 1829)

Specimens examined (2).—Wadi Al Kuf, mistnetted (1 ♀); Ruins, 6 km SE Qasr Maqdam (1 ♂).

Remarks.—The two specimens listed above and a third individual collected at Gharian, Libya, agree with specimens of *Plecotus austriacus* from Europe in external and cranial measurements, color of pelage, and shape of bacula. However, they are darker in color and larger in size than the holotype of *P. austriacus christie*, and specimens from Egypt and Giarabub Oasis in Libya referred to this subspecies by Lanza (1960), Harrison (1964), and Hanak (1966). The determination of the subspecific status of the Libyan specimens requires more comparative study.

Miniopterus schreibersii schreibersii (Kuhl, 1819)

Specimens examined (3).—Unnamed cave, Wadi Al Kuf (3 ♀♀).

Remarks.—This is the first record of *Miniopterus schreibersii* from Libya. This widespread species occurs from South Africa across Africa to Morocco and then across Europe as far as Australasia. External and cranial measurements and color of pelage of the three specimens agree with those of specimens from Europe and northeast Africa (the nominate subspecies) rather than with those of the Eastern Mediterranean region referable to *M. s. pallidus*.

Family Molossidae

Tadarida teniotis (Rafinesque, 1814)

Specimens examined (12).—Wadi Al Kuf, mistnetted (8 ♂♂, 4 ♀♀).

Remarks.—These are the first specimens of *Tadarida teniotis* recorded from Libya. They are referred, on geographic reasons, to *T. teniotis rueppellii* Temminck, the subspecies found in Morocco, Algeria, Egypt, and elsewhere in the Middle East.

One adult male with descended testes had testes measurements of 6.0 by 4.0. The range of measurements of testes of five other males was 2.0 to 3.0 in length and 1.1 to 2.0 in width.

DISCUSSION

The eight species of bats recorded from Jabal Al Akhdar fall into two general groups based on their zoogeographic distribution—Pale-arctic species or species with primarily Eurasian distributions but which also occur in North Africa to varying degrees and Cosmopolitan species or species with broad Eurasian and African distributions. The Pale-arctic species are *Rhinolophus mehelyi*, *Pipistrellus pipistrellus*, *Nyctalus lasiopterus*, *Plecotus austriacus*, and *Tadarida teniotis*. The Cosmopolitan species include *Rhinolophus clivosus*, *Pipistrellus kuhlii*, and *Miniopterus schreibersii*. The specimens of *Nyctalus lasiopterus* are the first records for the species for the African continent. *Plecotus austriacus* is known from as far south as Ethiopia in the East and Senegal and Cape Verde Islands in the West (Hayman and Hill, 1971).

In spite of the close proximity of the Jabal Al Akhdar to Egypt, only the specimens of *Rhinolophus mehelyi* and *Tadarida teniotis* show a close relationship with Egyptian populations. In the case of *Pipistrellus pipistrellus*, there seems to be little variation in external and cranial size and color of pelage around the whole of the Mediterranean. The *Nyctalus lasiopterus* of northeastern Libya seem to be closely related to populations of southcentral Europe. The *Rhinolophus clivosus* of northeastern Libya are larger than populations from neighboring North African countries. *Miniopterus schreibersii* and *Pipistrellus kuhlii* are similar to those from northwestern Africa and southern Europe.

The distributions and morphological attributes of the bats studied, and the characteristic Mediterranean Maquis type vegetation (Zohary, 1973:85), suggest that the bats of Jabal Al Akhdar are related to those of southcentral Europe and some probably reached this part of Libya by spreading across the islands of the central Mediterranean sea or are relicts of the more temperate climate (Hey, 1963) of the late Pleistocene/early Holocene in Cyrenaica.

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THE PLEISTOCENE (KANSAN) HERPETOFAUNA OF TROUT CAVE, WEST VIRGINIA

J. ALAN HOLMAN¹

ABSTRACT

A late Kansan herpetofauna recovered from the rear of Trout Cave, Pendleton County, West Virginia, includes at least two salamanders, three anurans, two lizards, and nine snakes. New material of the extinct salamander, *Cryptobranchus guildayi*, previously known only from a single dentary, is figured and discussed. The Trout Cave herpetofauna is generally similar to the late Kansan herpetofauna of Cumberland Cave, Maryland. Two snake species, *Elaphe vulpina*, and *Sistrurus catenatus*, do not occur in the region today, and may have reached the area by means of an ancient Prairie Peninsula Corridor.

INTRODUCTION

Recent excavations at Trout Cave, Pendleton County, West Virginia, have resulted in the recovery of only the second known herpetofauna of Kansan age from eastern United States. The other Kansan herpetofauna came from Allegany County, Maryland, about 129 km NNE of Trout Cave (Holman, 1977). Trout Cave lies in Pendleton County, West Virginia, at 38°36'14"N, 79°22'10"W, at an elevation of approximately 601 m, 5.6 km southwest of Franklin, West Virginia, on US Highway 220. The cave occurs in limestone of early Devonian age.

Fossils were collected by Frederick Grady in the autumn of 1980. The new material came from the rear of the cave and should be dis-

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tinguished from other Carnegie Museum of Natural History material that came from entrance deposits of Trout Cave. John E. Guilday (*in litt.*, 18 May 1981) has provided the following information about Grady's collections from Trout Cave. The new material came from the rear of the cave below a 2.4 m drop at the end of a "tight crawl." The matrix was dry-screened for fossils. The collection included mammals, birds, reptiles, amphibians, fishes, *Neotoma* droppings, and *Celtis* seeds; it is thought to have resulted probably from an old woodrat-owl accumulation. Arvicolid, ochotonid, and geomyid remains suggest a fauna of late Kansan age, contemporaneous with the Cumberland Cave, Maryland, fauna.

I should here like to extend my appreciation to Frederick Grady and John E. Guilday for the opportunity to study these interesting herpetological fossils. Jane Kaminski made the drawings.

Following is a check-list of the Trout Cave fossil herpetofauna.

Class Amphibia

Order Caudata

Family Cryptobranchidae

Cryptobranchus guildayi Holman

Family Ambystomatidae

Ambystoma opacum (Gravenhorst)

Order Salientia

Family Bufonidae

Bufo americanus Holbrook

Family Ranidae

Rana sylvatica Le Conte

Rana cf. *R. pipiens* Schreber

Order Squamata

Family Iguanidae

Sceloporus undulatus (Latreille)

Family Scincidae

Eumeces fasciatus (Linnaeus)

Family Colubridae

Nerodia sipedon (Linnaeus)

Thamnophis sp.

Heterodon platyrhinos Latreille

Coluber constrictor Linnaeus

Elaphe vulpina (Baird and Girard)

Lampropeltis triangulum (Lacepede)

Family Viperidae

Agkistrodon contortrix (Linnaeus)

Crotalus horridus Linnaeus

Sistrurus catenatus (Rafinesque)

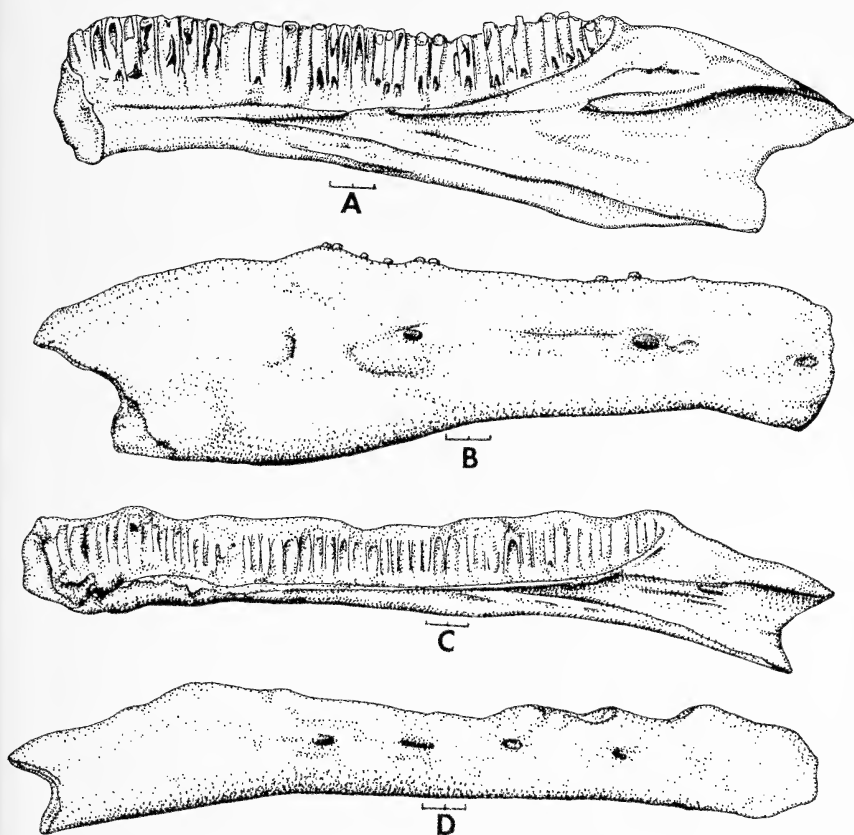


Fig. 1.—Right dentaries of *Cryptobranchus guildayi* from Trout Cave. A and C) lingual views; B and D) labial views. Each line equals 2 mm.

SPECIES ACCOUNTS

Following is an annotated list of the fossil herpetofauna of Trout Cave. Distributional data for modern amphibians and reptiles are from the maps of Conant (1975).

Class Amphibia
 Order Caudata
 Family Cryptobranchidae
Cryptobranchus guildayi Holman

Material.—Two right dentaries, one right epiphyal, one atlas, one nearly complete and one fragmentary trunk vertebrae, three fragmentary caudal vertebrae, two right femora, one right scapula, CM 40416.

Remarks.—This species was described on the basis of a single left dentary from the late Kansan Cumberland Cave fauna of Allegany County, Maryland (Holman, 1977). It was diagnosed as differing from the modern species, *C. alleganiensis*, in having (1) the Meckelian groove longer, (2) the dentary more weakly curved, and (3) a deeper groove on the labial border. The new material provides more information about this extinct form.

Dentary: The diagnostic longer labial groove is present in the two new fossil dentaries. They have the Meckelian groove extending the length of 34 tooth-alveolar spaces in a well-preserved specimen (Fig. 1a, b) and the length of 36 tooth-alveolar spaces in a second eroded and worn specimen (Fig. 1c, d). The type specimen of *C. guildayi* had the Meckelian groove extending the length of 34 tooth-alveolar spaces. The single available specimen of *C. alleganiensis* (MSU 13216) has this groove extending only the length of 24 tooth-alveolar spaces.

A second diagnostic character of the weaker curvature of the dentary, is also found in the new specimens. Both are more weakly curved than in *C. alleganiensis*. A third character, a deeper groove in the labial border of the dentary, is not supported by the new fossils which both have this groove similar in depth to *C. alleganiensis*.

Epihyal: The right epihyal bone is much different in *C. guildayi* than in the modern *C. alleganiensis* (Fig. 2). In the fossil there is a very strongly developed posterior process which is absent in the modern specimen. It seems that this process might be associated with different feeding habits in the fossil species. The epihyal does not ossify in the cryptobranchid genus *Andrias* (Meszoely, 1966).

Trunk vertebra: The single nearly complete trunk vertebra of *Cryptobranchus guildayi* from the Trout Cave site (Fig. 3) is shorter and wider than trunk vertebrae from the modern *C. alleganiensis*. This may be shown by comparing the ratio of the greatest width through the postzygapophyses divided by the greatest length through the zygapophyses in the fossil (0.69) to a sample of 18 trunk vertebrae of the modern *C. alleganiensis* (0.56–0.65, $\bar{x} = 0.602 \pm 0.021$).

Femur: In the fossil, the distal ridge is better developed and extends farther down the shaft than in *C. alleganiensis*. In *C. guildayi* the distal muscular line extends two-thirds the length of the shaft, in *C. alleganiensis* it extends only half the length of the shaft.

Scapula: The scapula of *C. guildayi* is differently shaped than in *C. alleganiensis* (Fig. 4). In *C. guildayi* the scapula has its dorsal surface more rounded and its posterior process making a greater angle with the shaft than in *C. alleganiensis*.

Revised diagnosis of Cryptobranchus guildayi: Because of the new material of *C. guildayi* from Trout Cave, it seems appropriate here to

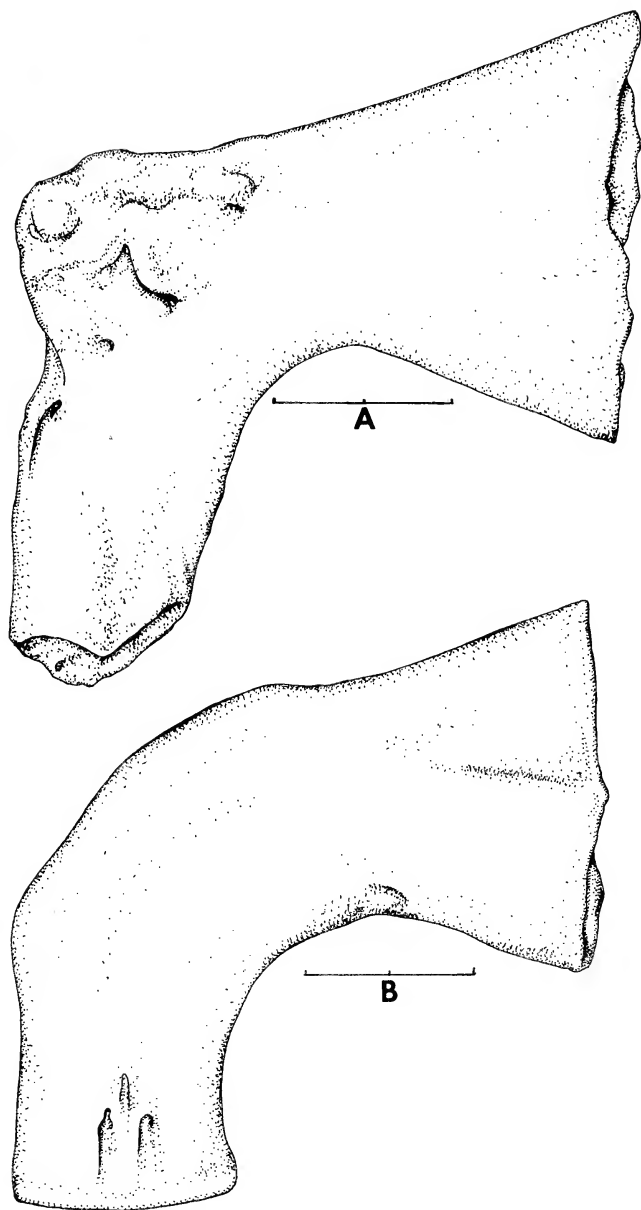


Fig. 2.—Epihyals of *Cryptobranchus*. A) *Cryptobranchus guildayi* from Trout Cave; B) *Cryptobranchus alleganiensis*. Each line equals 2 mm.

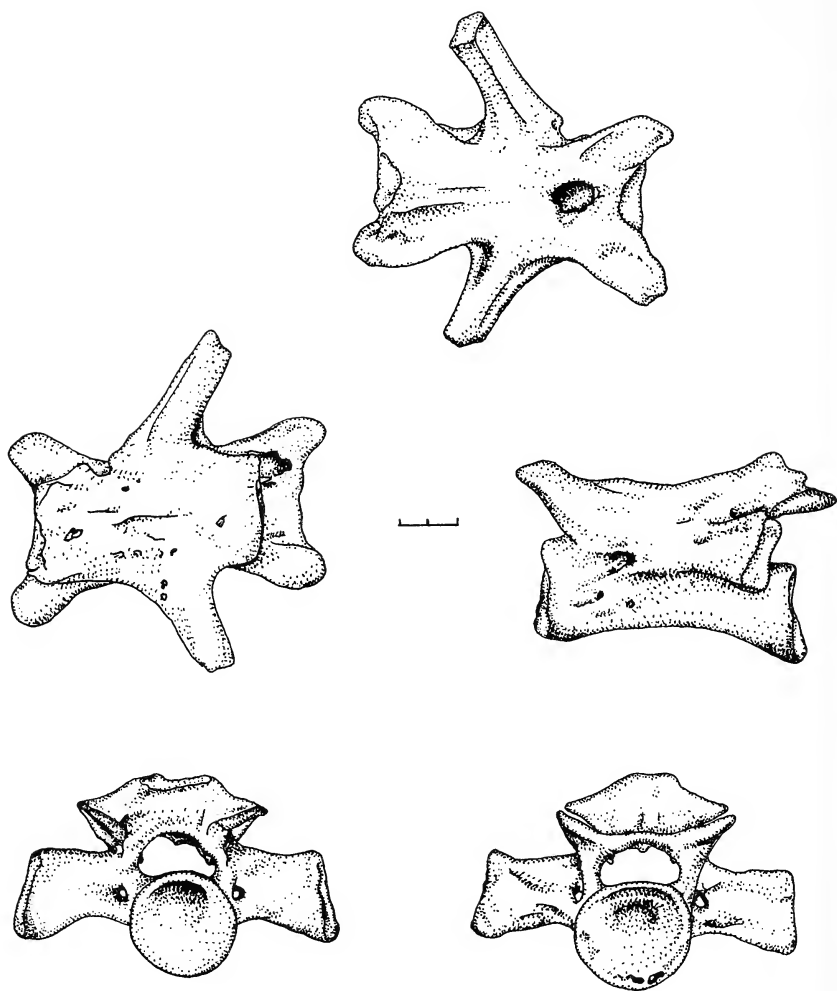


Fig. 3.—Trunk vertebra of *Cryptobranchus guildayi* from Trout Cave. Top, dorsal view; upper left, ventral view; upper right, lateral view; lower left, posterior view; lower right, anterior view. The line equals 2 mm.

present a revised diagnosis of this extinct species as follows: (1) dentary differs from *C. alleganiensis* in having a longer Meckelian groove and in being more weakly curved; (2) epihyal bone differs from *C. alleganiensis* in having a strongly developed posterior process (this process is lacking in *C. alleganiensis*); (3) the available trunk vertebra

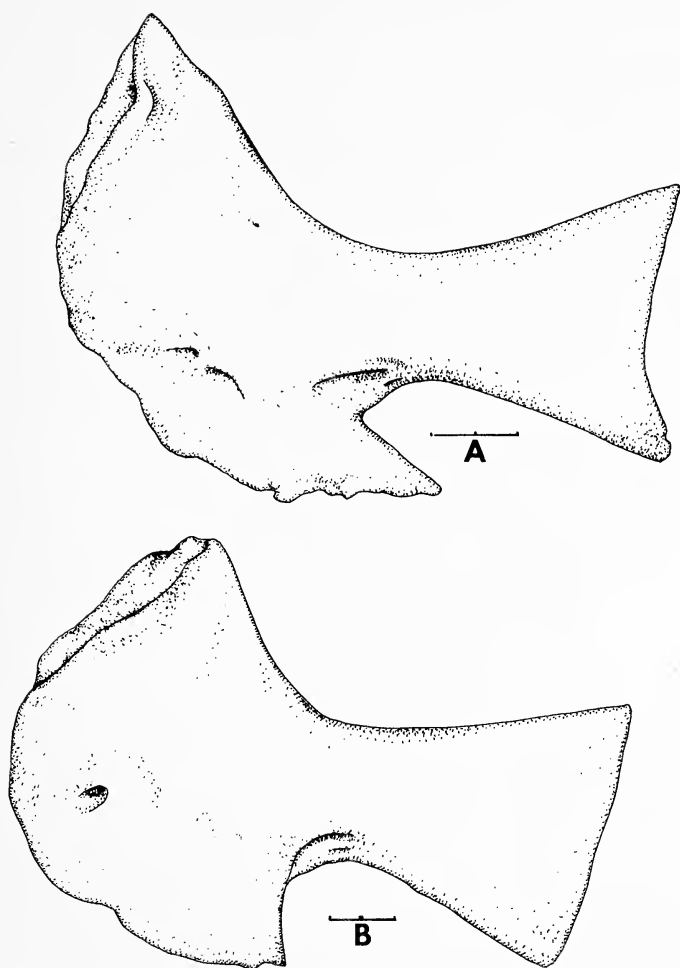


Fig. 4.—Scapulae of *Cryptobranchus*. A) *Cryptobranchus guildayi* from Trout Cave; B) *Cryptobranchus alleganiensis*. Each line equals 2 mm.

of *C. guildayi* is shorter and wider than those of *C. alleganiensis*; (4) femur of *C. guildayi* has a much better developed and more extensive distal muscular line than in *C. alleganiensis*; (5) scapula of *C. guildayi* has its dorsal surface more rounded and with a greater angle between its posterior process and the shaft than in *C. alleganiensis*.

Naylor (1981) stated "Holman's (1977) *C. guildayi* from the Pleistocene (Kansan) of Maryland is probably referable to *C. alleganiensis*

(R. Estes, pers. comm.).'' Because Naylor and Estes have not seen the *C. guildayi* material, it would seem best to retain *C. guildayi* as a valid species until additional data are presented.

Cryptobranchus does not occur in Pendleton County, West Virginia, today, as it is restricted to that part of the state west of 79°30' (Conant, 1975).

Family Ambystomatidae
Ambystoma opacum (Gravenhorst)

Material.—Two trunk vertebrae, CM 40417.

Remarks.—Other than characters listed in Tihen (1958) and Holman (1977), the trunk vertebrae of *Ambystoma opacum* differ from those of *A. jeffersonianum* in being shorter and wider, and from *Ambystoma maculatum* in lacking the flared posterior portion of the neural arch. *Ambystoma opacum* lacks the posteriorly upswept neural arch of *A. tigrinum*. I cannot distinguish the Trout Cave vertebrae from those of *A. opacum*, a species that occurs in the area today.

Order Salientia
Family Bufonidae
Bufo americanus Holbrook

Material.—One left ilium, CM 40418.

Remarks.—Holman (1977) referring to Holman (1967) and Wilson (1975) stated that the ilia of *Bufo americanus* may be separated from those of *B. woodhousei* in that the base of the dorsal protuberance is wider in *B. americanus* than in *B. woodhousei*. Another character that appears to separate these two species is that the dorsal protuberance in *B. americanus* is deflected more anteriorly than in *B. woodhousei*. *Bufo americanus* occurs in the area today.

Family Ranidae
Rana sylvatica LeConte

Material.—Two right ilia, CM 40419.

Remarks.—The ilia of *Rana sylvatica* may easily be distinguished from other species of *Rana* of eastern United States on the basis of the following combination of characters: (1) its small size; (2), a vastus prominence with a pronounced tubercle; (3) the posterodorsal border of the ilial crest sloping precipitously into the dorsal acetabular expansion. *Rana sylvatica* occurs in the area today.

Rana cf. *Rana pipiens* Schreber

Material.—Right ilium, CM 40420.

Remarks.—This ilium with a smooth vastus prominence and with the posterodorsal border of its ilial crest sloping gently into the dorsal acetabular expansion, appears identical to those of the northern leopard frog, *Rana pipiens*. But as far as I can determine there are no consistent differences between the ilia of any of the "leopard frog" species (*R. pipiens*, *R. blairi*, *R. berlandieri*, and *R. utricularia*), thus I shall only tentatively assign this ilium to the northern species, *R. pipiens*. No leopard frogs have been reported in the area today (Conant, 1975) although there seems to be no reason why they should not occur there.

Order Squamata

Family Iguanidae

Sceloporus undulatus (Latreille)

Material.—One fairly complete right dentary and three fragmentary left dentaries; one left humerus, CM 40421.

Remarks.—The above material is indistinguishable from skeletal material of *Sceloporus undulatus*, the species that occurs in the area today.

Family Scincidae

Eumeces fasciatus (Linnaeus)

Material.—Left dentary, CM 40422.

Remarks.—This dentary has a tooth-alveolar count of 25, falling within the range of *E. fasciatus* and outside of the range of *E. anthracinus* and *E. laticeps* (Holman, 1981:51, Table 1). I can find no differences between the fossil and dentaries of skeletons of *E. fasciatus*, a species that occurs in the area today.

Family Colubridae

Nerodia sipedon (Linnaeus)

Material.—Two trunk vertebrae, CM 40423.

Remarks.—Holman (1967) discussed the basis on which individual vertebrae of *Nerodia sipedon* may be distinguished from other species of *Nerodia*. This species occurs in the area today.

Thamnophis sp.

Material.—Nineteen trunk vertebrae, CM 40424.

Remarks.—These elongate natricine vertebrae are assigned to *Thamnophis* rather than to *Nerodia* based on the criteria of Brattstrom (1967). I cannot determine the species represented based on these fragmentary vertebrae.

Heterodon platyrhinos Latreille

Material.—Three trunk vertebrae, CM 40425.

Remarks.—These vertebrae have the depressed neural arch and wide, flat hemal keel that is characteristic of the genus *Heterodon*. They represent a much larger form than the modern *H. simus*, and appear to be identical in size and in characters to the species *H. platyrhinos*, a form that occurs in the area today.

Coluber constrictor Linnaeus

Material.—Seven trunk vertebrae, CM 40426.

Remarks.—These vertebrae are not distinguishable from those of modern *C. constrictor*, a species that is found in the area today. Based on geographic and altitudinal grounds the vertebrae are assigned to *C. constrictor* rather than to the species *C. flagellum*, a form that has very similar vertebral characters.

Elaphe vulpina (Baird and Girard)

Material.—Eleven trunk vertebrae, CM 40427.

Remarks.—This species of *Elaphe* is distinguished from others in the genus on the basis of its lower neural spine (Fig. 5a). Today this species occurs as two disjunct subspecies. One occurs in the marshy lands around portions of Lake Erie and Lake Huron. The other occurs from northwestern Indiana and western northern Michigan through Wisconsin and northern Illinois, southern Minnesota, Iowa, and the glaciated regions of Missouri west to southeastern Nebraska. Thus, the Trout Cave record is much to the east of the modern range of the species. This species was also found in the Pleistocene (late Kansan) of Cumberland Cave, Allegany County, Maryland.

Lampropeltis triangulum (Lacepede)

Material.—Six trunk vertebrae, CM 40428.

Remarks.—This species has trunk vertebrae with low neural spines and depressed neural arches and may easily be distinguished from related species. This species occurs in the area today.

Family Viperidae

Agkistrodon contortrix (Linnaeus)

Material.—Three trunk vertebrae, CM 40429.

Remarks.—The trunk vertebrae of *Agkistrodon* (Fig. 5b, c) may be distinguished from those of *Sistrurus* and *Crotalus* on the basis of those characters given below in the *Crotalus horridus* section. *Agkistrodon contortrix* usually can be distinguished from *A. piscivorus* trunk

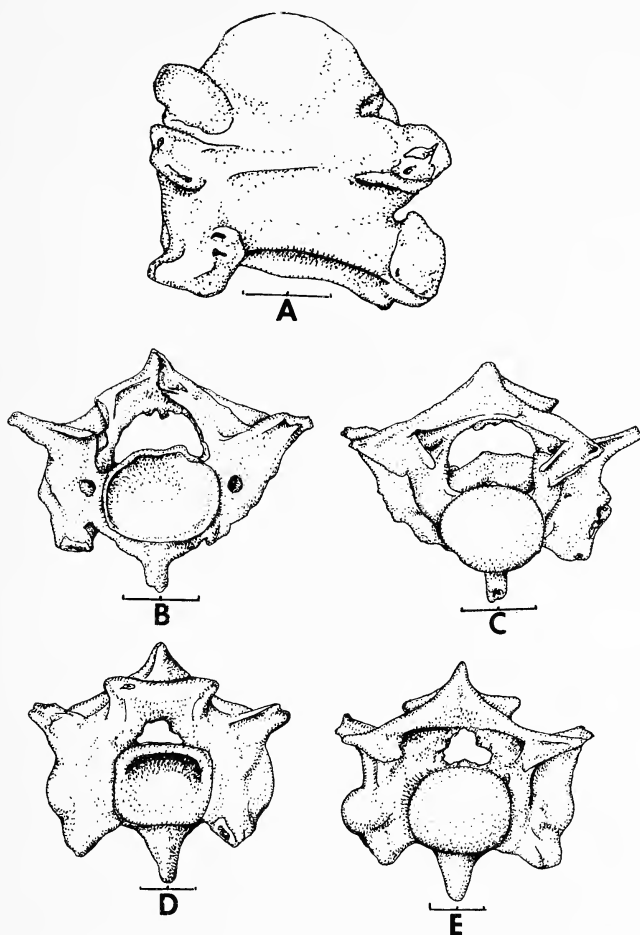


Fig. 5.—Trunk vertebrae of fossil snakes from Trout Cave. A) *Elaphe vulpina* in lateral view; B) *Agkistrodon contortrix* in anterior view; C) posterior view; D) *Crotalus horridus* in anterior view; E) posterior view. Each line equals 2 mm.

vertebrae on the basis of the smaller size, lower neural spine, less vaulted neural arch, and smaller cotylar foramina. *Agkistrodon contortrix* occurs in the area today.

Crotalus horridus

Material.—Fourteen trunk vertebrae, CM 40430.

Remarks.—The trunk vertebrae of *Crotalus horridus* (Fig. 5d, e) has a lower neural spine, and a less vaulted neural arch than *Sistrurus*.

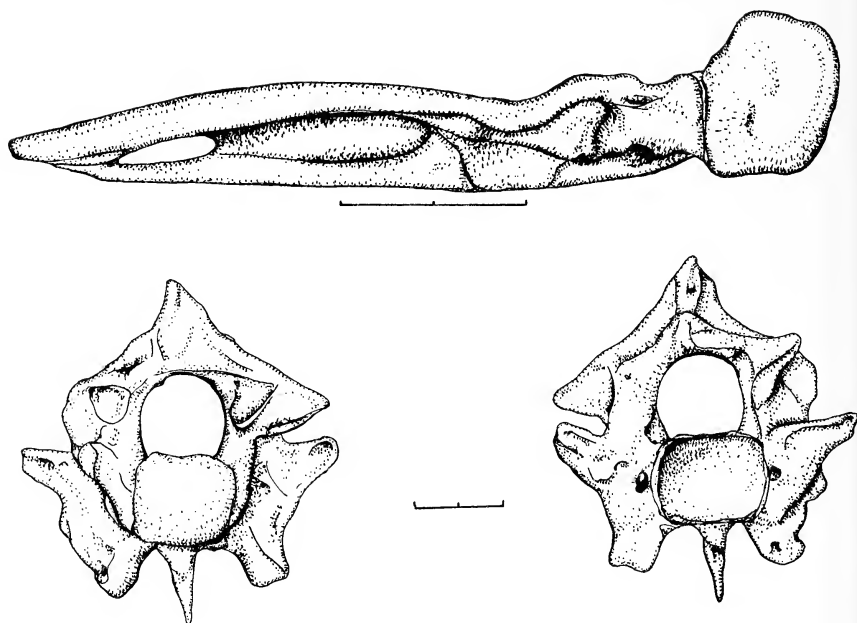


Fig. 6.—Fossils of *Sistrurus catenatus* from Trout Cave. Top, left posterior mandible (compound bone) in dorsal view; bottom left, trunk vertebra in posterior view, right, anterior view. Each line equals 2 mm.

The trunk vertebrae of *Crotalus horridus* have a lower neural spine, a less vaulted neural arch, and smaller cotylar foramina than in *Agkistrodon piscivorus*. *Crotalus horridus* may be distinguished from *Agkistrodon contortrix* on the basis of its much larger size and from *C. adamanteus* and *C. atrox* on the basis of the much lower neural spine. *C. horridus* occurs in the area today.

Sistrurus catenatus (Rafinesque)

Material.—Left compound bone, seven trunk vertebrae, CM 40431.

Remarks.—The compound bone (Fig. 6 top) of *Sistrurus catenatus* (4) has a retroarticular process which is quite blunt in dorsal view, thus differing from *Agkistrodon bilineatus* (1), *A. contortrix* (4), *A. piscivorus* (7), *Crotalus adamanteus* (4), *C. atrox* (7), *C. horridus* (8), and *C. viridis*. *Sistrurus catenatus* has the retroarticular process blunter than in *S. miliarius* (3), and both the fossil and modern mandibles of *S. catenatus* are larger than in *S. miliarius*.

The posterior mandible of *Sistrurus catenatus* lacks a lateral tuber-

cle just posterior to the quadrate notch. This tubercle is very strong in *S. miliarius*, is moderately prominent in *Agkistrodon bilineatus*, weak in *A. contortrix*, very prominent in *A. piscivorus*, and weak in *Crotalus horridus*.

Auffenberg (1963) has pointed out that the vertebrae of *Sistrurus* have a small spine or prominence just anterior to the neural spine that is lacking in *Crotalus* or *Agkistrodon*. Unfortunately, the fossil vertebrae (Fig. 6 bottom) are too fragmentary to observe this character. But I have observed that *Sistrurus* vertebrae have a more vaulted neural arch than in *Agkistrodon contortrix* and *Crotalus horridus*.

Sistrurus catenatus does not occur in West Virginia today, and the possible significance of the fossil occurrence will be mentioned in the discussion section.

DISCUSSION

Although the number of species is fewer (16 compared to 30), the Trout Cave Kansan herpetofauna is generally similar to that of the Cumberland Cave, Maryland, Kansan herpetofauna. With the exception of *Agkistrodon contortrix* and *Sistrurus catenatus*, all of the species represented at Trout Cave are present at Cumberland Cave (Holman, 1977:158–159). Moreover, as in the Cumberland Cave herpetofauna, the Trout Cave assemblage is one that would be found in the area today with the exception of a few species. Two of these Trout Cave species occur quite a distance west of the area today; two occur rather near, but have not been reported from the modern fauna of Pendleton County, West Virginia.

The fox snake, *Elaphe vulpina*, now occurs in marshes on the eastern border of Lake Huron and the northern border of Lake Erie. The massasauga, *Sistrurus catenatus*, occurs in the central part of westernmost Pennsylvania. These modern distributions are within 435 km and 250 km respectively of Trout Cave. The encroachment of grassland (or westerly marshland) species into the Cumberland Cave herpetofauna was postulated by Holman (1977) to be related to the extension of a Prairie Peninsula Corridor (see Schmidt, 1938; Smith, 1957) wedged between the northern coniferous forest and the southern deciduous forest (Holman 1977:fig. 3). The range of *Elaphe vulpina* and *Sistrurus catenatus* appears to follow the remnants of the Prairie Peninsula Corridor today; and this corridor can be envisioned as having extended even farther east to eastern West Virginia in Kansan times. The hellbender, *Cryptobranchus*, and the leopard frog, *Rana pipiens*, do not occur in Pendleton County, West Virginia, today, but have been recorded from several miles away (Conant, 1975). Perhaps this recent distribution may be attributed to the presence of the proper aquatic or marshy habitats for these species in late Kansan times and the lack of these habitats in modern times.

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ARTICLE 21

THE BRAINCASE OF A SMALL SAUROPOD DINOSAUR (REPTILIA: SAURISCHIA) FROM THE UPPER CRETACEOUS LAMETA GROUP, CENTRAL INDIA, WITH REVIEW OF LAMETA GROUP LOCALITIES

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ABSTRACT

The greater part of the braincase of a small sauropod dinosaur from the Upper Cretaceous Lameta Group near Dongargaon, Central India, is described. The braincase most closely resembles that of *Antarctosaurus septentrionalis*, the only other sauropod from the Lameta Group for which a substantial portion of braincase has been described. Differences between the two braincases are regarded as too great, however, to consider them as belonging to the same genus or species and the Dongargaon braincase is referred to the suborder Sauropoda as indeterminate. A variety of vertebrates, including fish, turtles, and dinosaurs, are now known from the Lameta Group near Dongargaon and the fauna as a whole is considered to be Santonian to Maastrichtian in age and to indicate a probable continental facies. A review of the Lameta Group localities of India is also given.

INTRODUCTION

Cretaceous dinosaurs from the Indian subcontinent are extremely rare and are known almost exclusively from the Upper Cretaceous

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Lameta Group of western and central India. Some fragmentary remains of dinosaurs are known also from the Ariyalur beds of equivalent age near Trichinopoly, southern India (Yadagiri and Ayyasami, 1979). The first authoritative account of Upper Cretaceous dinosaurs of India was given by Lydekker (1877). He erected a new genus and species of sauropod, *Titanosaurus indicus*, on the basis of two posterior caudal vertebrae, a chevron, and a femur from the Lameta Group near Jabalpur (Fig. 1), and also described a tooth from the Ariyalur beds as probably belonging to the theropod *Megalosaurus*; neither specimen was illustrated. Falconer (1868), however, did describe both caudal vertebrae without naming them and provided excellent illustrations of one. Lydekker (1879) redescribed the type of *T. indicus*, with figures of the vertebrae, and the *Megalosaurus* tooth was also figured. In the same paper he described and figured some caudal vertebrae as referable to a new species of *Titanosaurus*, *T. blanfordi*, and a chevron as referable to *Titanosaurus* sp. from the Lameta Group near Pisdura (Fig. 1). Nearly a half century later Matley (1923) described fragmentary postcranial remains of what he believed to be a new genus and species of stegosaur, *Lametosaurus indicus*, from the Lameta beds near Jabalpur (=Jubbulpore of other authors), but later reassessed it as an ankylosaur (Huene and Matley, 1933). It is very likely that the dermal scutes of the type of *L. indicus* belong to a titanosaurid sauropod, possibly *Titanosaurus indicus*, and the remainder of the skeleton to one or more theropod dinosaurs (Chakravarti, 1935; Walker, 1964; Sues, 1980; Galton, 1981). Yet, Galton (1981) cautions that Huene and Matley (1933) mentioned, but did not figure, two additional types of dermal scutes from the Lameta beds that could be ankylosaurian. Chakravarti (1933) described a new genus and species of stegosaur, *Brachypodosaurus gravis*, from the Lameta beds near Jabalpur (Chota Simla) on the basis of a humerus. Galton (1981) has remarked, however, that it is not only difficult to identify it as a humerus from the photographs, but also whether it is stegosaurian or ankylosaurian. Huene and Matley (1933) described the first, large assemblages of dinosaurs from the Lameta Group. These were collected by Matley near Jabalpur and Pisdura between 1917 and 1920. Included among the described materials were sauropods, allosaurid carnosaurs, coelurosaurs, and the type of *L. indicus*; the sauropods were described by Huene and Matley; the theropods by Huene, and the type of *L. indicus* by Matley. The sauropods included *Titanosaurus indicus*, *T. blanfordi*, *Antarctosaurus septentrionalis* sp. nov., and *Laplatasaurus madagascariensis*. From a specific site near Jabalpur, referred to as the "sauropod bed" of Bara Simla Hill, Huene and Matley sorted out a large collection of almost entirely disassociated sauropod elements which they concluded belonged to at least three individuals, probably four

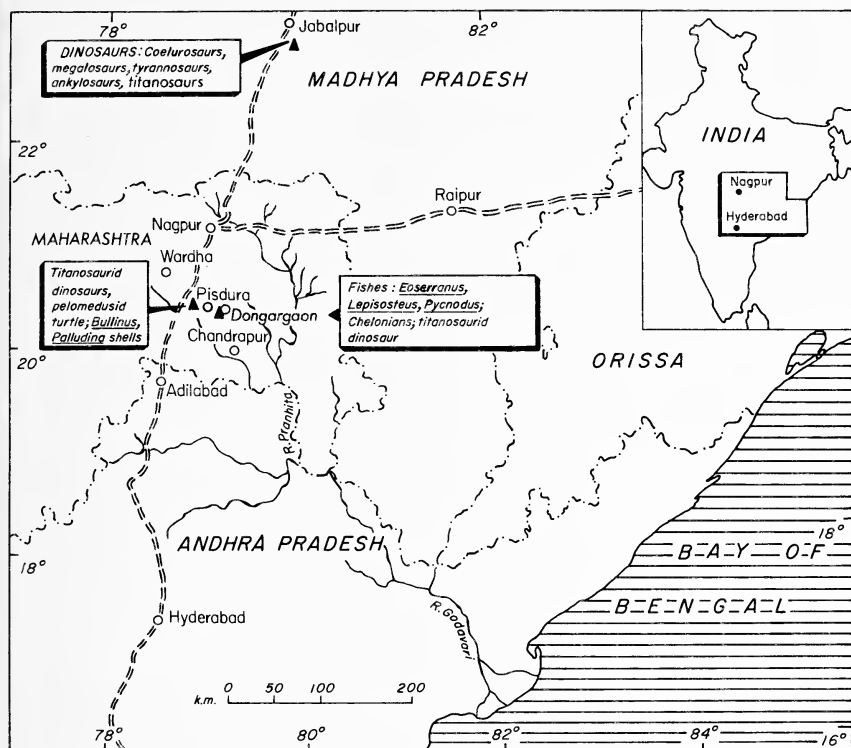


Fig. 1.—Map of central India showing collecting localities of the Upper Cretaceous Lameta Formation.

or even five, of two different genera and species. Caudal vertebrae, hemapophysis, and damaged tibia and fibula were referred to *Titanosaurus indicus*, the type of which came from the same site. Huene and Matley also showed that the femur included in the type of *T. indicus* by Lydekker (1877) came from a bed other than that of the type locality and probably pertained to *Antarctosaurus*. A portion of braincase, left squamosal, hyoid, and numerous postcranial elements from the "sauropod bed" were made the basis of the new species *Antarctosaurus septentrionalis*. Separation of the skeletal elements of *A. septentrionalis* from those of other Lameta sauropods was based mainly on their larger size, more slender proportions, and close similarity to those of the Patagonian *Antarctosaurus wichmannianus*.

The braincase of *A. septentrionalis* is of particular interest, because until now it was the only substantial portion of sauropod skull known

from the Cretaceous beds of India. At a site near Dongargaon (Fig. 1), about 16 km east of the well known sauropod locality at Pisdura, field collecting parties of the Geological Studies Unit of the Indian Statistical Institute, Calcutta, have collected disassociated, well preserved dorsal and caudal vertebrae, and the greater part of an uncrushed braincase of sauropods. All of the specimens were found as surface finds or loosely embedded in green clays of the Lameta Group. The vertebrae, as yet undescribed, are very close to those of *T. indicus*. The braincase, which is the subject of this paper, is close to that of *A. septentrionalis* but considerably different from that of *A. wichmanianus*, and its assignment for the present is best viewed as indeterminate below the level of suborder Sauropoda. The braincase from Dongargaon also takes on added importance because that of *A. septentrionalis* has been either lost or misplaced. The Dongargaon braincase has been cataloged into the paleontological collections of the Indian Statistical Institute as R-199.

Abbreviations used in figures are as follows: af, articular facet for proatlas; Bo, basioccipital; Bs, basisphenoid; Eo, exoccipital; F, frontal; fm, foramen magnum; ica, foramen for internal carotid artery; Ls, laterosphenoid; Os, orbitosphenoid; P, parietal; pa, foramen for palatine artery; pf, pituitary fossa; pn, foramen for palatine branch of facial nerve; pp, paroccipital process; Pr, proötic; So, supraoccipital; I-XII, foramina for cranial nerves.

GEOLOGY, FAUNA, AND AGE OF THE LAMETA GROUP

The Lameta Group of Central India is generally considered as a post-Gondwana deposit. It ranges from about 7 to 50 m in thickness and is best exposed and developed in its type area near Jabalpur in the eastern part of the Narmada Valley. The Lameta Group has been discussed by various workers and considerable confusion centers on whether it is marine or non-marine in origin. In brief considerations of the paleoecology of the Lameta beds, Matley (1921), Pascoe (1964), Sahni (1972), and Sahni and Mehrotra (1974) favored a freshwater origin. Their assessments were based primarily on the presence of freshwater and terrestrial invertebrates and vertebrates from the Lameta Group as a whole, rather than on sedimentological studies. Chanda (1966, 1968), on the other hand, has redefined the Lameta Group and the Jabalpur Group, which underlies it in their type area, and has given a detailed sedimentological analysis of their paleoecology. He observed that limestone, which is absent in the Jabalpur Group, constitutes practically the whole of the Lameta Group. Further, the sandstone and white clay of the Jabalpur Group are viewed as representing a typical flood plain model, whereas the sediments of the Lameta Group are viewed as characterizing shallow marine deposition. Most importantly, Chanda noted the occurrence of autochthonous glauconite and algal stro-

matolites, along with low amounts of clastic detritus. He viewed this as indisputable evidence that the Lameta beds were deposited in inner neritic marine waters on the stable shelf of the western margin of the low lying Indian craton where they received generally a slow, but at times variable, supply of terrigenous materials. Chanda also argued that the rare occurrences of terrestrial and freshwater fossils found in the Lameta beds, most associated with conglomeratic levels, were washed in from outside along with other debris and, therefore, are of no value in interpreting the Lameta environment. Robinson (1967), on the other hand, concluded that the Lameta beds represent an admixture of marine near shore, possible lagoonal and continental facies in the Jabalpur region, but a mainly continental facies west and south of Jabalpur. The fact that many of the vertebrate bones of the Lameta deposits of Jabalpur are too well preserved to have been transported far is viewed by Robinson as evidence of occasional, brief episodes of continental conditions.

Upper Cretaceous dinosaurs from the Lameta Group of Central India are best known from two widely separated areas, that near Jabalpur, Bara Simla Hill, and the other near Pisdura, Pisdura Hill (Fig. 1). Of the two areas, the Jabalpur fauna from the eastern part of the Narmada Valley is represented by a much greater variety of dinosaurs based on more complete and better preserved specimens, and, as a consequence, has received far greater attention. The dinosaurs occur at various levels in the Lameta beds of the Jabalpur area (Matley, 1921), but, as pointed out by Robinson (1967), important occurrences are restricted to two distinct levels of probably significantly different ages at Bara Simla Hill. In his revision of the stratigraphy of the Lameta Group near Jabalpur, Chanda (1968) recognized three formational units—a lower Greensand which rests unconformably on the Jabalpur Group or Precambrian crystallines; a middle Lower Limestone; an Upper Sandy Limestone which is succeeded by the Deccan Trap basalts. From a pocket eroded into the top of the Greensand at Bara Simla Hill, commonly referred to as the "carnosaur pocket," have come a very few sauropod remains of *Titanosaurus* and indeterminate sauropods, but most importantly several carnosaurs, including *Indosuchus raptorius*, *Indosaurus matleyi*, and coelurosaurs (Huene and Matley, 1933; Chatterjee, 1978). The type of *Lametasaurus indicus* and testudine turtles are also known from this site (Huene and Matley, 1933). The other significant dinosaur site at Bara Simla Hill near Jabalpur, referred to as the "sauropod bed," occurs about 1.3 m above the Lower Limestone in the Upper Sandy Limestone and consists of red and green marly clay (Matley, 1921); the "sauropod bed" and "carnosaur pocket" are about 13 m apart. With the exception of rare fragments of an indeterminate carnosaur, the sauropod bed can be

contrasted with the carnosaur pocket as having yielded otherwise only the titanosaurs *Titanosaurus indicus* and *Antarctosaurus septentrionalis* (Huene and Matley, 1933). Huene and Matley (1933) considered the age of the Lameta dinosaurs of Jabalpur as a whole to be Turonian. The presence of the large carnosaurs, thought by them to all be megalosaurs (=allosaurs), was the primary basis for their age determination, because megalosaurs are not known to occur in the later part of the Upper Cretaceous. Robinson (1967) agreed with Huene and Matley on a Turonian age for the fauna of the carnosaur pocket. However, she judged the sauropod bed fauna to represent probably a younger age, perhaps Santonian or even later, because the titanosaurs are closely comparable, as also noted by Huene and Matley (1933), with Maastichtian Patagonian forms. On the basis of his reassessment of *Indosuchus raptorius* as a tyrannosaurid, rather than an allosaur, Chatterjee (1978) estimated the age of the lower third of the Lameta Group to be at least younger than Turonian, inasmuch as tyrannosaurids occur in the highest Cretaceous, most notably the Lance Formation of North America. More precisely, he suggested a Santonian age for this level because *Indosaurus matleyi* is a highly advanced megalosaur and *Indosuchus raptorius* is a highly primitive tyrannosaurid. Walker (1964) was the first to recognize *I. raptorius* as a primitive tyrannosaurid and his reassignment has been accepted by other authors (Steel, 1970; Rozhdestvenskii, 1977; Olshevsky, 1978). Molnar (1980), however, claims that the described materials exhibit no incontrovertible tyrannosaurid features.

The Lameta fossil locality near Pisdura, Pisdura Hill, is about 320 km south of Jabalpur. In this region in the state of Maharashtra, the Lameta Group occurs as disjunct exposures and the age of each should be determined independently on the basis of the fossils it contains (Robinson, 1967). Fossils at Pisdura occur in a thick bed of red clay with rare green bands that lies beneath the Deccan Trap basalts. Invertebrates from this locality include the molluscs *Bullinus (Physa) prinsepii*, *Paludina deccanensis*, and indeterminate forms; the presence of the former species has created some controversy as to the stratigraphic position and age of the producing beds. *B. prinsepii*, not seen elsewhere in the Lameta beds, is typical of the mainly early Tertiary, freshwater deposits intercalated between the overlying Deccan Trap basalts, referred to as the Intertrappean beds. The occurrence of *B. prinsepii* at Pisdura Hill led Pascoe (1964) to suggest that, though the locality is Infratrappian in position, lying below the Deccan Trap, it may be Intertrappean in age. However, as Robinson (1967) points out, Pascoe (1964) has recorded *B. prinsepii* in beds yielding a Maastichtian marine fauna in Northern Baluchistan. Titanosaurids from Pisdura, all represented by a few elements or fragments, include *Ti-*

tanosaurus blanfordi, *Titanosaurus* cf. *T. indicus*, *Laplatasaurus* cf. *L. madagascariensis*, and *Antarctosaurus* sp. (Huene and Matley, 1933). A freshwater pelomedusid turtle skull, *Carteremys pisdurensis*, and an undescribed plastron and carapace have also been recorded from this locality (Jain, 1977). Huene and Matley (1933) ascribed a Turonian to Santonian age to the Pisdura locality mainly on the basis that *L. madagascariensis* occurs in beds of this age in Madagascar and the Pisdura titanosaurs are similar to those of the sauropod bed of Jabalpur. Robinson (1967) assessed the Pisdura fauna as Santonian in age, but cautioned that the presence of *B. prinsepii* may suggest an age as young as Maastrichtian. In this context, it is worth noting, as Huene and Matley (1933) did, that all three Pisdura titanosaur genera are found in beds ranging from upper Senonian (Coniacian to Campanian of some authors) to Maastrichtian in South America. In view of the presence of the pelomedusid turtle *C. pisdurensis*, titanosaurid dinosaurs, and the molluscs *B. prinsepii* and *P. deccanensis*, Jain (1977) concluded that the Pisdura locality is not younger than Upper Cretaceous and represents at least in part a freshwater environment. The paleoenvironment map presented by Robinson (1967:241, Fig. 7) of the post-Gondwana (Turonian through Maastrichtian) phase of deposition in India shows the Lameta beds west and south of Jabalpur, which includes Pisdura Hill and the Dongargaon locality discussed below, as representing continental facies.

Localities near Dongargaon and nearby Dhamni (latter not shown in Fig. 1) are known for the fish fossils described by Woodward (1908) which include one teleostean, *Eoserranus hislopi*, and two ganoids, *Lepisosteus indicus* and *Pycnodus lametae*. Woodward placed the age of the fish fauna between the Upper Cretaceous Danian and the Upper Eocene, which indicated to him an Intertrappean rather than an Lameta horizon. Matley (1921) described the Dongargaon beds as not only quite distinct from those of the type Lameta Group, but those at Pisdura as well, and as consisting of greenish and brownish clays with bands of white and cream-colored limestones exposed below the Deccan Trap basalts. He considered the Dongargaon beds as Intertrappean in age, though not in position, and therefore not part of the Lameta Group. During 1968 and 1969 and subsequent years field collecting parties of the Geological Studies Unit of the Indian Statistical Institute, Calcutta, recovered numerous testudinid turtle plastra-carapace and dinosaur bones, mainly as surface finds, from green Lameta clays of the Dongargaon locality. The small sauropod braincase described here is a part of this collection, as well as vertebrae which closely resemble those of *Titansaurus indicus* described by Huene and Matley (1933) from Jabalpur. Until more detailed paleontological studies now in progress are completed, the Dongargaon fauna as a whole is considered as

Santonian to Maastrichtian in age and as probably indicating a continental facies.

DESCRIPTION
(Figs. 2-7)

The braincase from Dongargaon is typical of sauropods in its form and general features. It lacks mainly the cultriform process of the parasphenoid, basal tuberi, basiptyergoid processes and the distal ends of the paroccipital processes. In posterior view (Fig. 2) the occiput was undoubtedly subrectangular in outline. As preserved the occiput is formed by the basioccipital, exoccipitals, supraoccipital, and parietals. The sutural contacts of the exoccipital with the supraoccipital and opisthotic are completely fused and not traceable. It is assumed that the original limits of the exoccipital exposure on the occiput included at least the area between the lateral rim of the foramen magnum and the base of the paroccipital process, and the extreme posterolateral corner of the lateral wall of the braincase enclosing the opening for cranial nerve XII (Figs. 4, 5). On either side of the foramen magnum is a circular, boss-like protuberance that was undoubtedly the site of articulation of the vertebral proatlas. On the basis of conditions in other sauropods (Berman and McIntosh, 1978), the supraoccipital probably formed the dorsal margin of the foramen magnum; the exoccipital-supraoccipital contact probably extended laterally from the foramen magnum just above the articular facet for the proatlas as a broadly undulating suture that ended at the post-temporal fenestra (not preserved in this specimen). The opisthotic undoubtedly formed most, if not all, of the occipital exposure of the paroccipital process. In sauropods the exoccipital-opisthotic suture is commonly absent, apparently fusing early. The contact between the exoccipital and the basioccipital is traceable only on the articular surface of the occipital condyle, where it appears as a shallow, weathered channel across the dorsolateral corner of the condyle. The basioccipital forms most of the articular surface of the occipital condyle. The condyle is convex posteriorly and ventrally, and slightly concave dorsally. The axis of the condyle is directed strongly posteroventrally (Figs. 4, 5). The angle subtended between the long axis of the condyle and the plane of the occipital surface is about 120° , indicating that the skull was probably oriented at nearly a right angle to the vertebral column as in *Diplodocus* and *Apatosaurus*, and apparently in *Antarctosaurus wichmanianus* and *A. septentrionalis* (Huene, 1929; Huene and Matley, 1933; Berman and McIntosh, 1978). Though incompletely preserved, the nuchal crest of the supraoccipital is very massive. The occipital exposure of the paired parietals was apparently extensive.

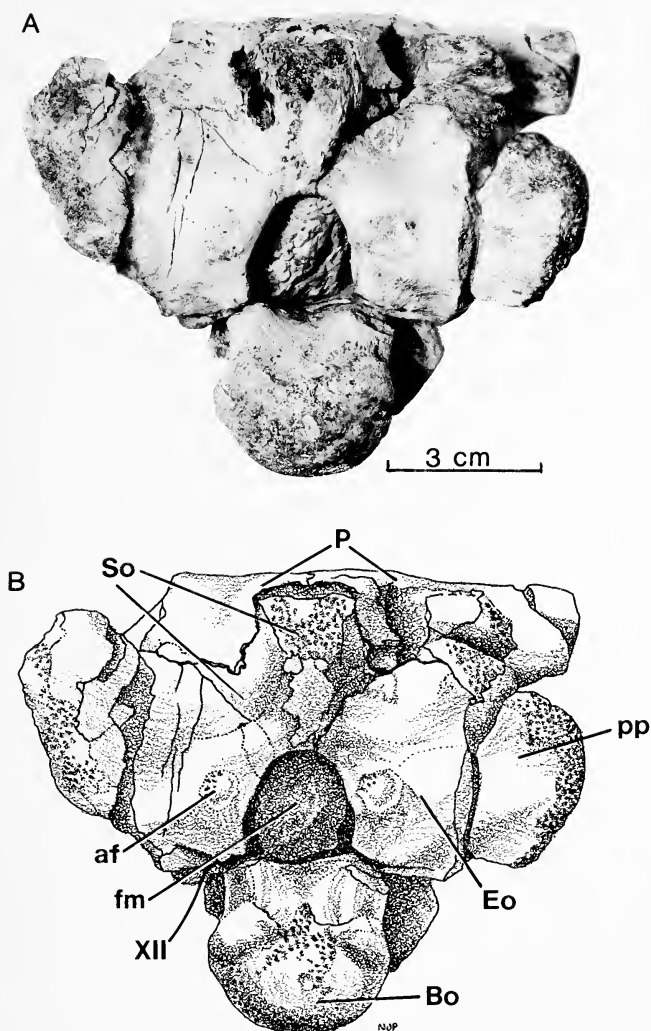


Fig. 2.—(A) Photograph and (B) illustration of Dongargaon sauropod braincase R-199 in occipital view.

In dorsal view (Fig. 3) the broad, flat parietals and frontals dominate the Dongargaon braincase roof. Their midline suture is very tightly closed. The parietal-frontal suture is not obvious, but there is a scar-like, textured line that reveals its transverse course across the skull

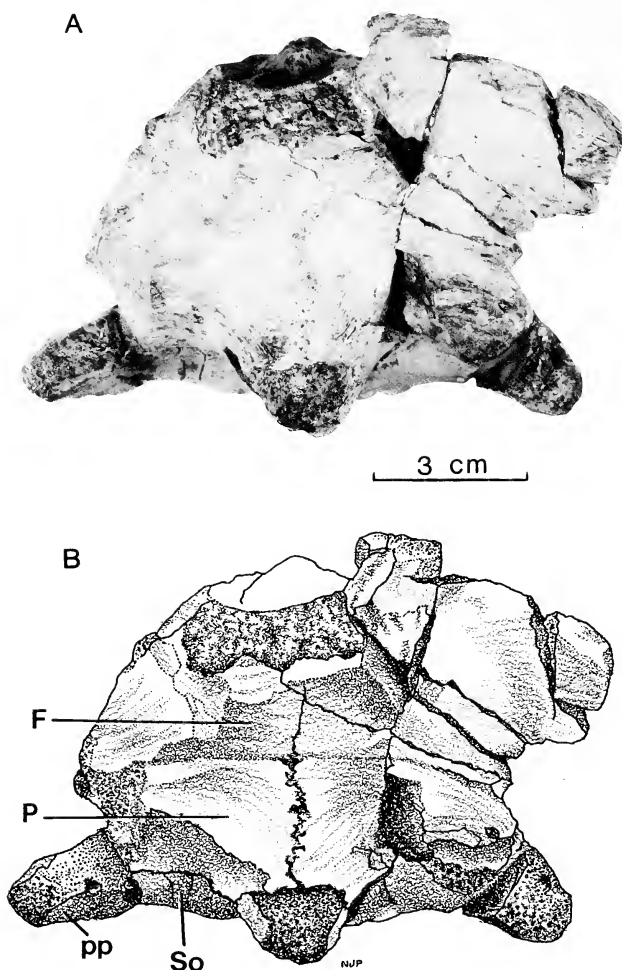


Fig. 3.—(A) Photograph and (B) illustration of Dongargaon sauropod braincase R-199 in dorsal view.

roof at the level of the uppermost end of the supratemporal fossa, preserved only on the right side. This position of the parietal-frontal suture is consistent with that of most sauropods.

The right and left passages for cranial nerve XII are exposed in a wide, transverse break in the thick neck of bone connecting the ball-like condyle with the braincase proper (Figs. 4, 5). Just ventral to the base of the paroccipital process on the lateral wall of the braincase is

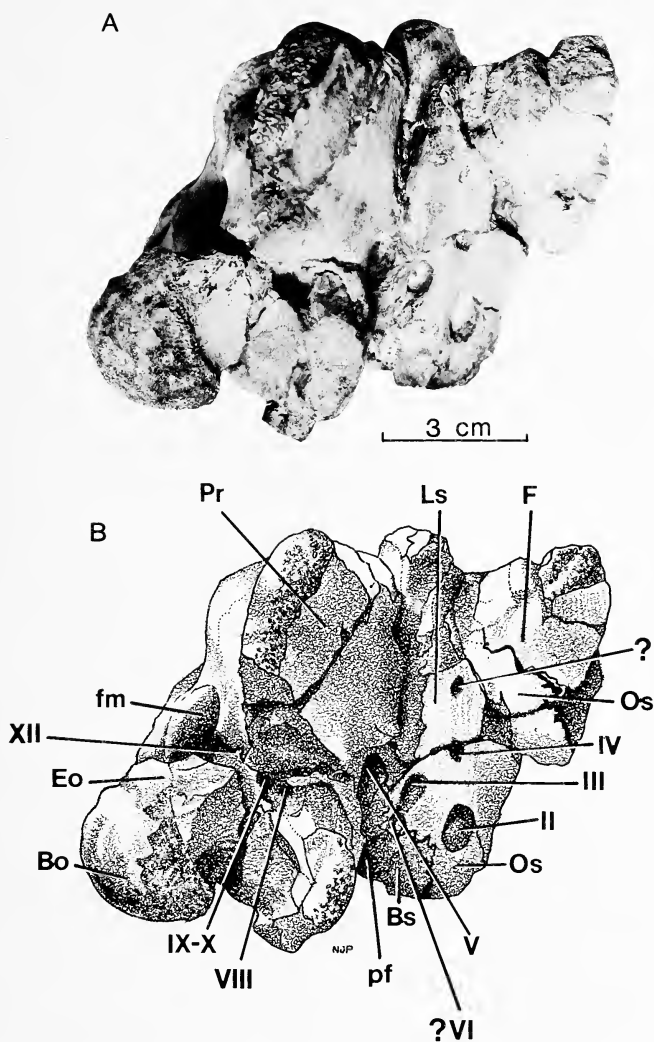


Fig. 4.—(A) Photograph and (B) illustration of Dongargaon sauropod braincase R-199 in right lateral view.

a very large, deep cavity, the boundaries of which are poorly defined on both sides of the braincase due to breakage. At the bottom of the cavity are two large openings; almost surely the larger posterior opening transmitted nerves IX–X and probably the jugular vein, and the smaller anterior opening cranial nerve VIII. On the left side of the

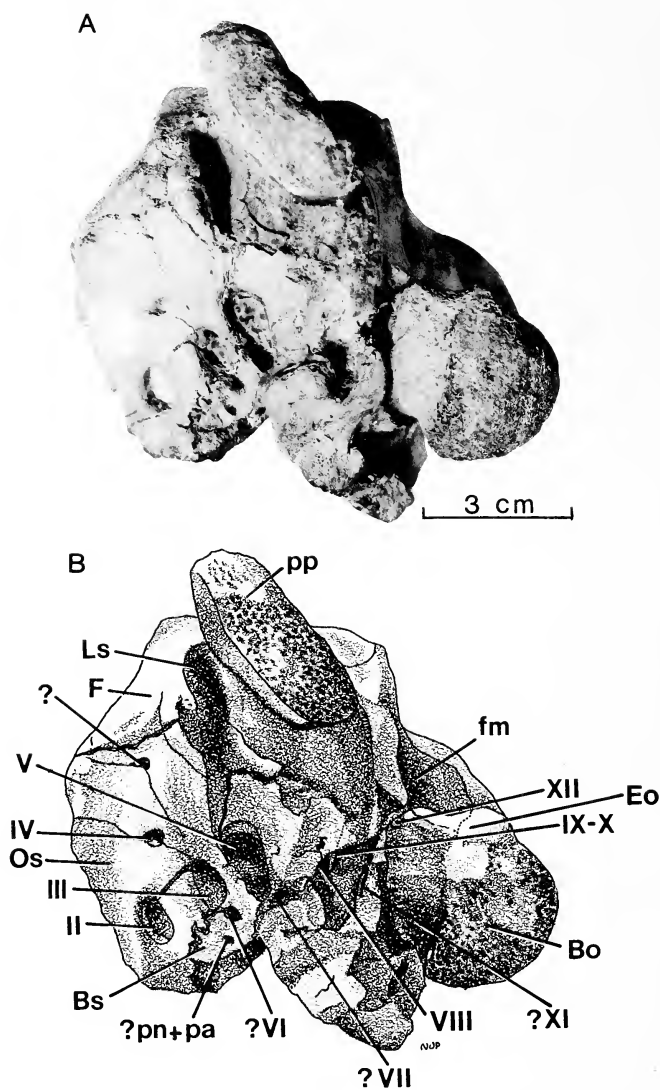


Fig. 5.—(A) Photograph and (B) illustration of Dongargaon sauropod braincase R-199 in left lateral view.

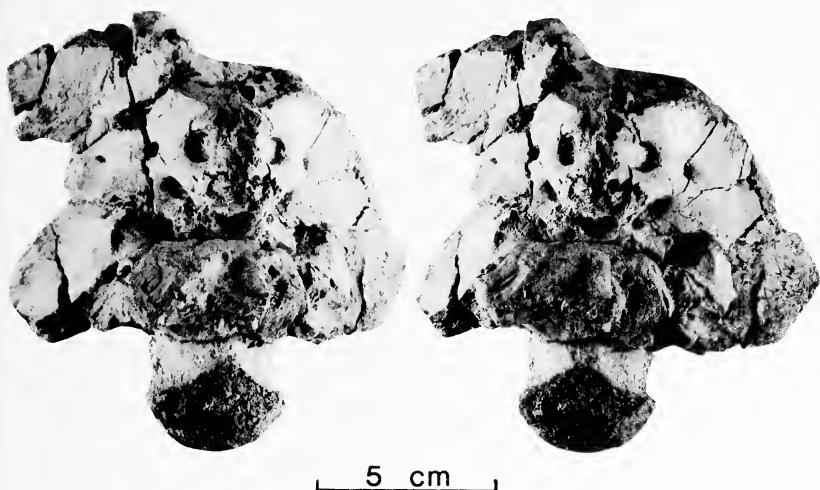


Fig. 6.—Dongargaon sauropod braincase R-199 in ventral view (stereo pair).

braincase (Fig. 5) loss of bone along the posterior wall of the cavity has exposed a very small canal that may have held cranial nerve XI. There is no sign of a opisthotic-proötic suture. The opening for cranial nerve VIII, however, is typically positioned on this suture near, or at, its intersection with the basisphenoid. The proötic undoubtedly formed the anterior face of the preserved portions of the paroccipital processes, and its contact with the laterosphenoid anteriorly is well marked by a long, vertical abutment suture. The large exit for nerve V is positioned on the boundary between the proötic and laterosphenoid just above the basisphenoid. The foramen for the VII nerve, which typically perforates the proötic a short distance anterior to cranial nerve VIII, cannot be identified with any certainty. What may be this foramen is a poorly defined opening a short distance posterior to the ventral end of the foramen for nerve V on the left side of the braincase.

The laterosphenoid and orbitosphenoid, the anteriormost two elements of the lateral wall of the braincase, form a broad, flat, antero-laterally facing surface (Figs. 4–7). They are completely fused together without any trace of a suture; their contacts with the frontal and basisphenoid, however, are very clear. It is reasonable to suspect that the laterosphenoid-orbitosphenoid contact originally extended along a line passing through the openings for cranial nerves III and IV as it does in *Diplodocus* and *Apatosaurus* (Berman and McIntosh, 1978). The thick, incomplete posterolateral edge of the laterosphenoid pro-

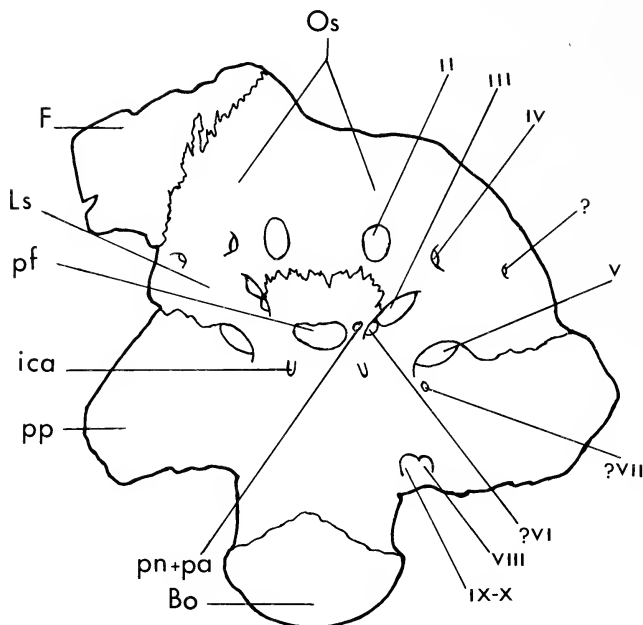


Fig. 7.—Outline sketch of ventral view of Dongargaon sauropod braincase R-199 of Fig. 6.

jects a short distance laterally from the braincase wall. In other sauropods the laterosphenoid expands outward as it extends dorsally, forming a thick, laterally arching lamina of bone, the crista antotica, that contacts the ventromedial edge of the portion of postorbital forming the anterior wall of the supratemporal fossa (White, 1958; Berman and McIntosh, 1978). Above the foramen for nerve IV and just below the frontal is an opening of unknown function. Almost merging with the ventral margin of the large foramen for nerve III and just within the basisphenoid is an opening that may have been for the passage of cranial nerve VI. This foramen is best seen on the left side of the braincase (Fig. 5), where the basisphenoid is complete enough to also exhibit a small foramen that may have been for the palatine branch of the facial nerve and the palatine branch of the carotid artery. The very large opening for nerve II is completely surrounded by the orbitosphenoid, which extends anteriorly a short distance beyond the foramen to merge with its mate. The incompleteness of the basisphenoid has exposed the passages for the paired internal carotid arteries at an internal level and the pituitary fossa through its ventral floor (Figs. 6, 7).

COMPARISONS

To date, the only sauropod braincase material known from the Upper Cretaceous Lameta Group of India is that described by Huene and Matley (1933) as belonging to *Antarctosaurus septentrionalis*. Unfortunately, it is even less complete than the braincase described here from Dongargaon. Despite this, it is apparent that, whereas the two braincases are very similar, differences of sufficient magnitude do exist to suggest that the Dongargaon braincase may pertain to a species or genus other than *A. septentrionalis*.

It is interesting that despite the small size of the Dongargaon braincase, almost all of the sutures are absent or barely detectable due to their great degree of closure. In the braincase of *A. septentrionalis*, which is almost twice as large as that from Dongargaon, the closure and loss of sutures has proceeded to a greater extent, to include also the supraoccipital-parietal suture of the occiput and the parietal-frontal and midline sutures of these two skull roof elements; age may account for this difference. The height of the supraoccipital, measured from the top of the foramen magnum, is not greater than the height of the foramen magnum in *A. septentrionalis*, whereas in the Dongargaon specimen the height of the supraoccipital is much greater. The distinct articular facet for the proatlas on the exoccipital of the Dongargaon braincase is a feature not only absent in *A. septentrionalis*, but also not noted in any other sauropod. The nuchal crest of the supraoccipital in the Dongargaon braincase is far more massively developed than in *A. septentrionalis*.

In *A. septentrionalis* the anteroposterior extent of the skull roof posterior to a transverse line connecting the uppermost ends of the supratemporal fossae, which undoubtedly approximates the original parietal-frontal suture, is relatively much shorter than in the Dongargaon braincase; the anteroposterior extent of the parietal on the skull roof is, therefore, apparently much greater in the Dongargaon specimen. Huene and Matley (1933) described a high, sharp ridge on the parietal of *A. septentrionalis* that runs transversely between the upper ends of the supratemporal fossae along the posterior edge of the skull roof. There is no sign of development of such a ridge in the braincase described here. A moderately high buttress ridge below the paroccipital process is also described by Huene and Matley in *A. septentrionalis* as extending between the openings for the cranial nerves IX–X and VIII. In contrast, these two openings in the Dongargaon braincase are located at the bottom of a large, deep cavity.

Huene and Matley (1933) briefly compared the braincase of *A. septentrionalis* with that of *Antarctosaurus wichmannianus* described by Huene (1929) from the Upper Cretaceous of Patagonia. They concluded that only minor differences separated the two braincases. However,

even a superficial comparison clearly shows that the Dongargaon and *A. septentrionalis* braincases are far more similar to each other than either is to *A. wichmannianus*.

Of the few complete sauropod braincases that have been described in detail, those of the Jurassic *Diplodocus* and *Apatosaurus* (Berman and McIntosh, 1978) most closely approach that from Dongargaon; in their overall morphology they are very similar. Noteworthy features they have in common include: 1) similar extent and configuration of the parietal on both the dorsal roof and occiput of the braincase; 2) long axis of the occipital condyle directed strongly posteroventrally at about 120° from the plane of the occipital surface; 3) abutment suture between the the proötic and laterosphenoid (this suture tightly closed in probable braincase of type of *Apatosaurus ajax*, Berman and McIntosh, 1978); 4) apparent development of the posterolateral margin of the laterosphenoid into a laterally projecting, wing-like structure (also described in *Camarasaurus* by White, 1958); 5) identical topographic positions of almost all of the cranial nerve openings; and 6) development of a massive nuchal crest of the supraoccipital. The most prominent features that distinguish the Dongargaon braincase from those of *Diplodocus* and *Apatosaurus* include: 1) presence of well developed articular facets on the exoccipitals for the proatlases; 2) parietals are not fused to form a single element; 3) complete closure and loss, or apparent loss, of the sutures separating the exoccipital and supraoccipital, exoccipital and basioccipital (suture traceable only on occipital condyle), laterosphenoid and orbitosphenoid, and the parietal and frontal; 4) fused laterosphenoid-orbitosphenoid element forms a broad, flat, anterolaterally facing surface; 5) foramina of cranial nerves IX-X and VIII are located at the bottom of a large, deep cavity rather than on the outer surface of the braincase; and 6) cranial nerve VI appears to exit independently rather than through either the opening for the palatine artery and palatine branch of the facial nerve or that for cranial nerve III.

CONCLUSION

There is no doubt that the braincase described here from the Upper Cretaceous Lameta Group near Dongargaon, India, is referable to the suborder Sauropoda, but assignment below this level is at best uncertain. Because of the close resemblance between the Dongargaon braincase and that of the titanosaurid *Antarctosaurus septentrionalis* and the fact that all of the sauropods from the Lameta Group have been classified as titanosaurids, it might be considered reasonably safe to assign the Dongargaon braincase to the Titanosauridae. However, until more complete material is found it seems best to defer familial or lower taxonomic assignment of the Dongargaon braincase for several rea-

sons: 1) *Lameta* sauropods are very poorly known; 2) braincase anatomy is unknown or poorly known in most of the major groups of sauropods and in those where it is adequately known there appears to be little marked variation in structure; 3) the braincase of *A. septentrionalis* is quite distinct from that of *A. wichmannianus*, raising the possibility that it was incorrectly included in the type of *A. septentrionalis* and may not pertain to that genus.

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RESTUDY OF *MYCTEROSAURUS LONGICEPS* (REPTILIA, PELYCOSAURIA) FROM THE LOWER PERMIAN OF TEXAS

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ABSTRACT

Study of *Mycterosaurus longiceps* Williston from the Lower Permian (Leonardian) Clyde Formation of north-central Texas strongly suggests that this small pelycosaur is a primitive member of the family Varanopseidae. *M. longiceps* has been formerly included in the family Nitosauridae as a primitive edaphosaur and considered close to the ancestry of the caseids. This assignment was based almost exclusively on postcranial features recorded from a small portion of skeleton probably belonging to a temnospondylous amphibian, possibly a dissorophid, that was confused with a referred specimen. The possession by *M. longiceps* of several specialized features also suggests that it may represent an early divergent lineage from the central stock that comprises the other Permian varanopseids.

INTRODUCTION

The anatomy and systematic relationships of the small, carnivorous pelycosaur *Mycterosaurus longiceps* were last discussed in detail by Romer and Price (1940). Their study was based on several specimens, all from the Mitchell Creek nodular deposit of the Lower Permian

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(Leonardian) Clyde Formation, Clear Fork Group, of north-central Texas. The holotype (FMNH-UC 692), originally described by Williston (1915), consists of a nearly complete skull, some fragmentary vertebrae and a scapulocoracoid. A second specimen (AMNH 7002), consisting of a fragmentary skull and several portions of the postcranial skeleton, was described by Broom (1930) as *Eumatthevia bolli*; he was uncertain of its locality, except that it was from Texas. Romer and Price (1940) recognized not only that *Eumatthevia bolli* is a junior synonym of *Mycterosaurus longiceps*, but also that the former came from the same locality as the holotype. The earlier descriptions by Williston and Broom concentrated on the skull, and only a few general remarks were made about the postcranial skeleton. An additional specimen (FMNH-UC 169), consisting of a fragmentary skull and scattered postcranial materials, was described for the first time by Romer and Price (1940); this specimen was in great part the basis of their description of the postcranial skeleton.

The family Nitosauridae was erected by Romer and Price (1940) for the reception of *Nitosaurus jacksonorum* from the Lower Permian of New Mexico and *Mycterosaurus longiceps*. They placed the Nitosauridae in the suborder Edaphosauria, in which they also included the families Edaphosauridae, Lupeosauridae, and Caseidae. They considered the nitosaurids as primitive members of the suborder and close to the ancestry of the caseids. Nearly all of the features noted in *M. longiceps* to document this relationship were based on the postcranial skeleton, as they viewed the skull as simply representing a primitive level of pelycosaurian evolution. The most important of the edaphosaur features cited, however, were mistakenly recorded from an isolated portion of skeleton that was confused with one of the referred specimens (FMNH-UC 169). The misidentified specimen is not a pelycosaur but more likely a temnospondylous amphibian, possibly a disorophid. Reisz (1980) not only recognized this error, but also challenged the validity of *N. jacksonorum* and, thereby, the family Nitosauridae. The relationships of the families grouped by Romer and Price (1940) in the suborder Edaphosauria and even the validity of the family Lupeosauridae have also been questioned (Vaughn, 1958; Langston, 1965; Reisz, 1980). These observations have prompted the present paper.

Re-examination of all the *M. longiceps* specimens leads us to conclude that *Mycterosaurus* is best interpreted as a member of the family Varanopseidae (see Langston and Reisz, 1981, for explanation of formation and spelling of family name). This determination is based mainly on the skull, as the postcranial skeleton of *M. longiceps* provides little useful information for making taxonomic and phylogenetic associations. Generic assignment of the only other known species of

Mycterosaurus, *M. smithae*, described by Lewis and Vaughn (1965) from the Lower Permian Cutler Formation of Colorado, is here considered provisional. Further, specimens of *M. smithae* are too poorly preserved either to confirm or deny the assessment of the phylogenetic relationships of *Mycterosaurus* made by Romer and Price (1940) or this study. However, if *M. smithae* is correctly assigned to *Mycterosaurus*, then it is obviously more primitive than the somewhat later occurring *M. longiceps*. *Mycterosaurus* is viewed as representing, on the one hand, the most primitive level of structural organization within the Varanopseidae, and, on the other hand, as possibly an early offshoot from the lineage, or closely related lineages, that comprises the other Permian varanopseids.

Abbreviations AMNH, FMNH, MCZ, and USNM are used to refer to collections of the American Museum of Natural History, New York, Field Museum of Natural History, Chicago, Museum of Comparative Zoology, Harvard University, and the United States Museum of Natural History, respectively.

Key to abbreviations used in the figures:

a = angular	pf = postfrontal
as = astragalus	pm = premaxilla
bo = basioccipital	po = postorbital
c = calcaneum	pp = postparietal
co = coronoid	prf = prefrontal
d = dentary	pro = proötic
ep = epipterygoid	ps = parasphenoid
f = frontal	pt = pterygoid
fe = femur	ptf = posttemporal fenestra
fi = fibula	pu = pubis
h = humerus	q = quadrate
il = ilium	qj = quadratojugal
is = ischium	s = stapes
j = jugal	sa = surangular
l = lacrimal	sc = scapula
lj = lower jaw	so = supraoccipital
m = maxilla	scp = sclerotic plates
n = nasal	sq = squamosal
p = parietal	t = tibia

SYSTEMATIC PALEONTOLOGY

Class Reptilia

Subclass Synapsida

Order Pelycosauria

Family Varanopseidae Romer and Price, 1940

Revised diagnosis.—Small- to moderate-sized carnivorous pelycosaurs characterized by the following features: massive, deep maxillary process of premaxilla; elongate maxilla extends posteriorly well beyond level of postorbital bar; maxilla in contact with quadratojugal of

normal length to exclude jugal from ventral margin of skull; strongly recurved, flattened marginal dentition, extending beyond level of post-orbital bar; frontal with moderate contribution to orbital rim without development of lateral extension; large parapineal foramen located close to posterior edge of skull table; temporal fenestra enlarged and ventral arch reduced at least at its anterior end to a narrow bar; basicranial process of braincase with triangular outline in ventral view; occiput with large lateral process of supraoccipital and broad paroccipital process without recess for dorsal process of stapes.

Mycterosaurus Williston, 1915

Type species.—*Mycterosaurus longiceps* Williston, 1915.

Revised diagnosis.—Small varanopseid characterized by the following specialized features: greatly expanded dorsal lamina of maxilla excludes lacrimal from naris and shortens it to less than half the distance between orbit and naris; supraglenoid foramen absent; femur lacks internal and fourth trochanters and adductor crest; the anterior limiting ridge of the intertrochanteric fossa extends proximally without reduction nearly to the end of the femur. Differs from other varanopseids in the possession of the following primitive features: temporal fenestra not expanded posteroventrally; quadratojugal triangular in outline and excluded from temporal opening by jugal-squamosal contact; occiput and posterior edge of cheek nearly vertical with jaw joint at level of occipital condyle; presacral vertebrae with slightly excavated neural arches and centra lack ventral, midline keel; expanded anterior coracoid; massive lateral tubercle of pubis; astragalus with short neck and broad contact with fourth distal tarsal.

Mycterosaurus longiceps Williston, 1915

Holotype.—FMNH-UC 692, nearly complete skull, vertebral fragments, scapulocoracoid, proximal end of femur, distal end of humerus.

Referred specimens.—AMNH 7002, the type of *Eumatthevia bolli*, a damaged skull and scattered postcranial skeleton; FMNH-UC 169, partial skull and postcranial skeletal remains including three articulated segments of the vertebral column, pelvis and femur, scapulocoracoid and proximal half of humerus.

Horizon and locality.—All specimens from a red nodular layer in the Lower Permian (Leonardian) Clyde Formation, Clear Fork Group, near Mitchell Creek, Baylor County, north-central Texas. Mitchell Creek is a very small stream that drains into the Wichita River about 3.5 km east of where U.S. Highway 183-283 crosses the Wichita River.

Diagnosis.—Same as for genus [generic assignment of *M. smithae* Lewis and Vaughn, 1965, the only other described member of this

genus, is here considered questionable because the poorly preserved type exhibits none of the features which are diagnostic for this genus].

DESCRIPTION

Skull and lower jaw.—The restoration of the skull shown in Fig. 7 is based almost entirely on the holotype FMNH-UC 692 (Figs. 1–4, 5B); only the marginal dentition and the ventral margin of the skull roof are based on AMNH 7002 (Fig. 5A). The skull of the holotype has undergone extensive deformation, especially lateral compression, making the restoration of some aspects of the skull's gross morphology and proportions speculative. Many of the elements are represented, at least in part, as impressions of their internal surfaces and, although internal contacts between missing bones may be clearly preserved, there is usually considerable disparity between inner and outer surface patterns of the overlapping sutures. The occipital plate is incompletely preserved; the premaxilla, septomaxilla, tabular and supratemporal are absent. The restoration of the skull presented here differs from that given by Romer and Price (1940) in several important ways. This description is intended to emphasize mainly these differences, otherwise Figs. 1–7 are intended to take the place of a detailed description of the skull.

The orbit is unusually large and nearly circular; the rim bulges somewhat above the dorsal surface of the skull. Aside from a few small pits along the ventral margin of the maxilla, the only clearly discernable sculpturing patterns are a series of small, evenly spaced, transverse grooves along the dorsal orbital rim (FMNH-UC 692, FMNH-UC 169) and a series of about eight very small, closely spaced, tubercle-like ridges along the orbital rim of the jugal (AMNH 7002).

The premaxilla is preserved only in AMNH 7002 where the left premaxilla lacks only part of the dorsal ramus. The maxillary ramus is very large and deep, whereas the dorsal process, as indicated by its base, appears to have been slender. The maxilla is extremely long, extending from the ventral margin of the external naris along most of the ventral skull margin nearly to the midlength of the subtemporal bar where it narrowly contacts the quadratojugal. Above the largest maxillary teeth the dorsal lamina of the maxilla is greatly expanded, excluding the lacrimal from the naris; the lateral exposure of the lacrimal is reduced to less than half the distance between the orbit and the naris. The suborbital ramus of the lacrimal is reduced, and it is uncertain whether a narrow lacrimal-jugal contact is present. The upper marginal dentition, as seen in AMNH 7002 (Fig. 5A), consists of three premaxillary and 23 maxillary teeth that are very closely spaced, strongly recurved, sharply pointed and flattened from side to side. The

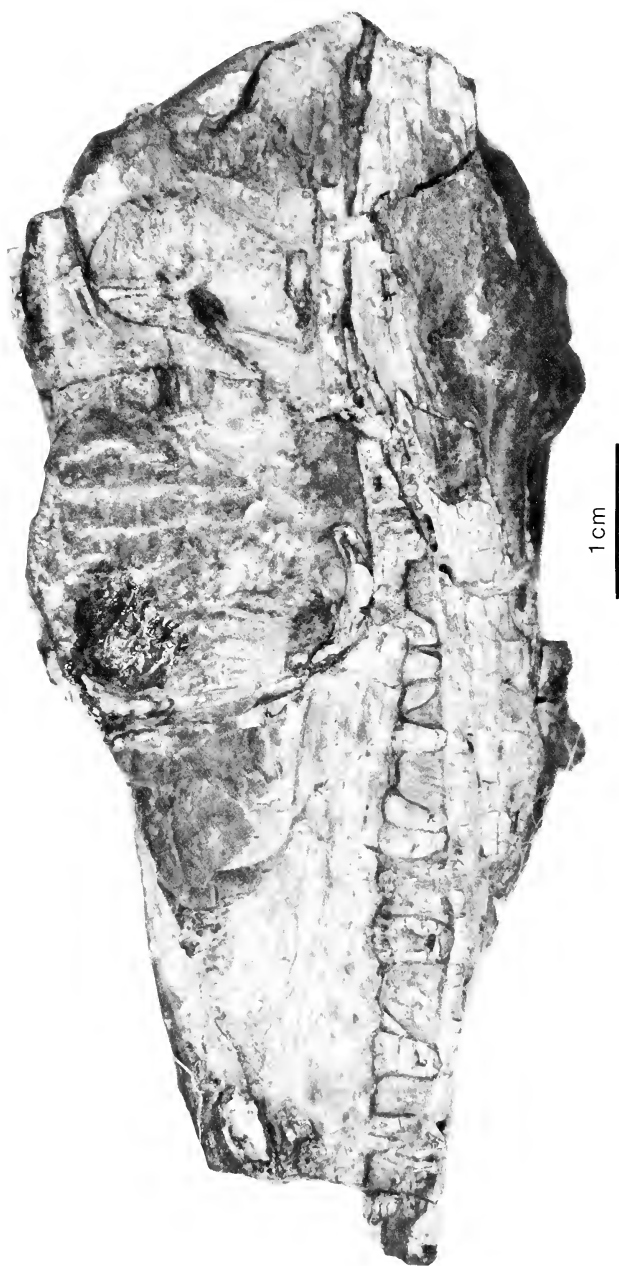


Fig. 1.—*Mycterosaurus longiceps*, holotype, FMNH-UC 692; photograph of skull in left lateral view.

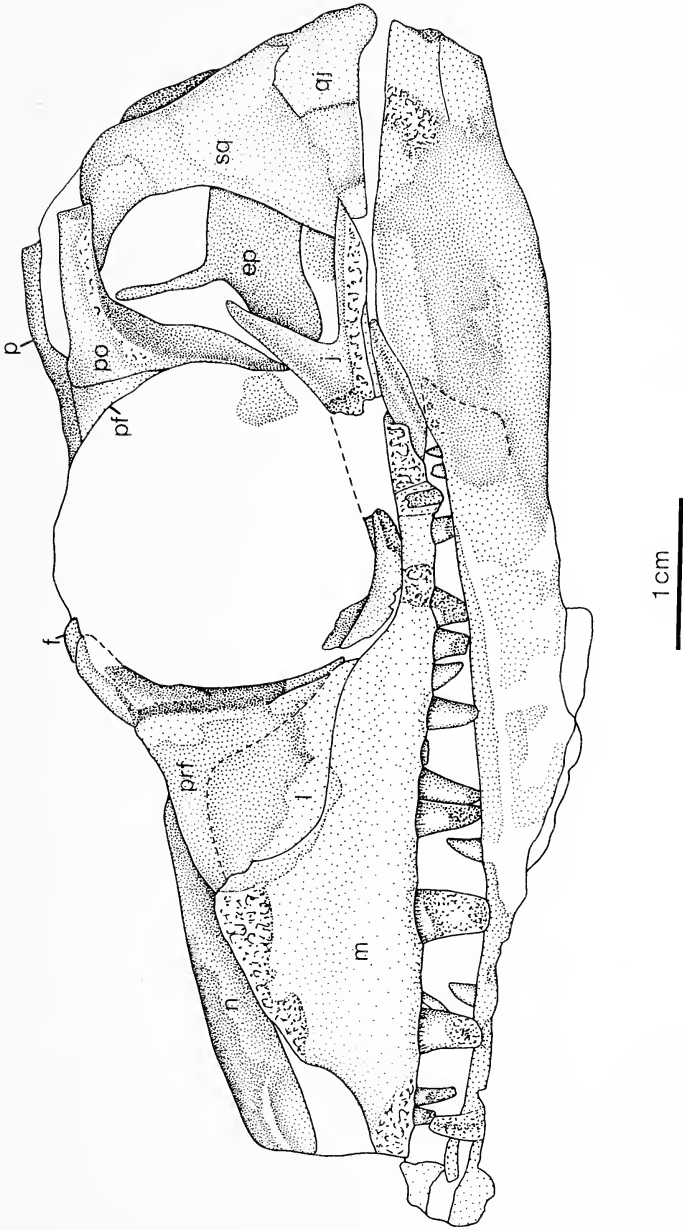


Fig. 2.—*Mycterosaurus longiceps*, holotype, FMNH-UC 692 as seen in Fig. 1.

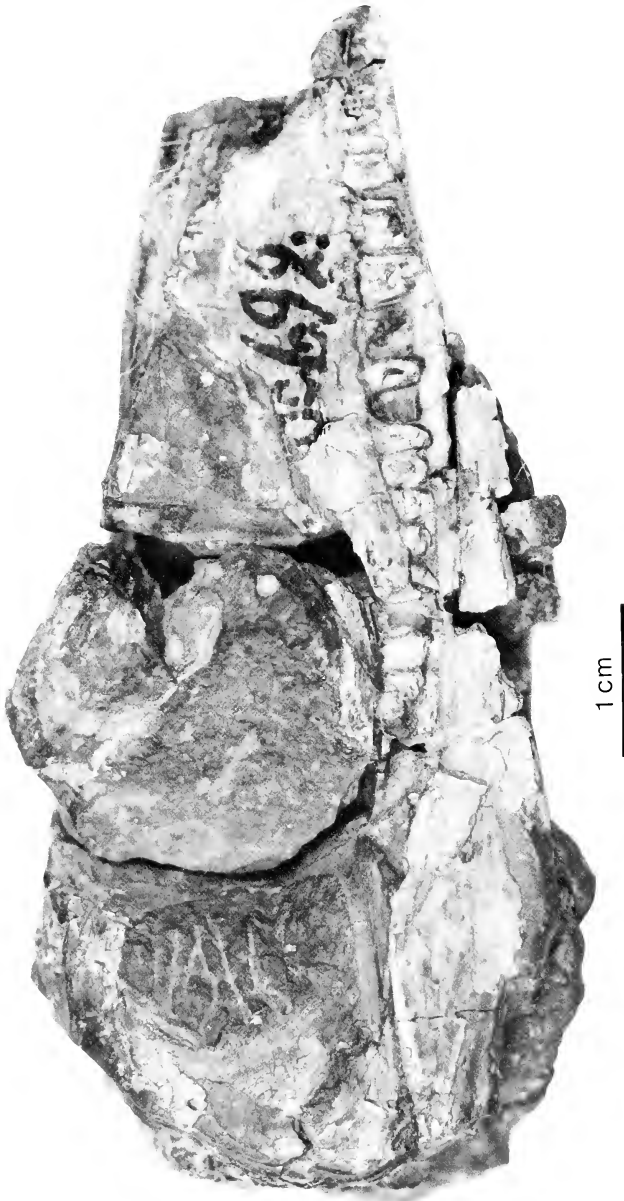


Fig. 3.—*Mycterosaurus longiceps*, holotype, FMNH-UC 692: photograph of skull in right lateral view.

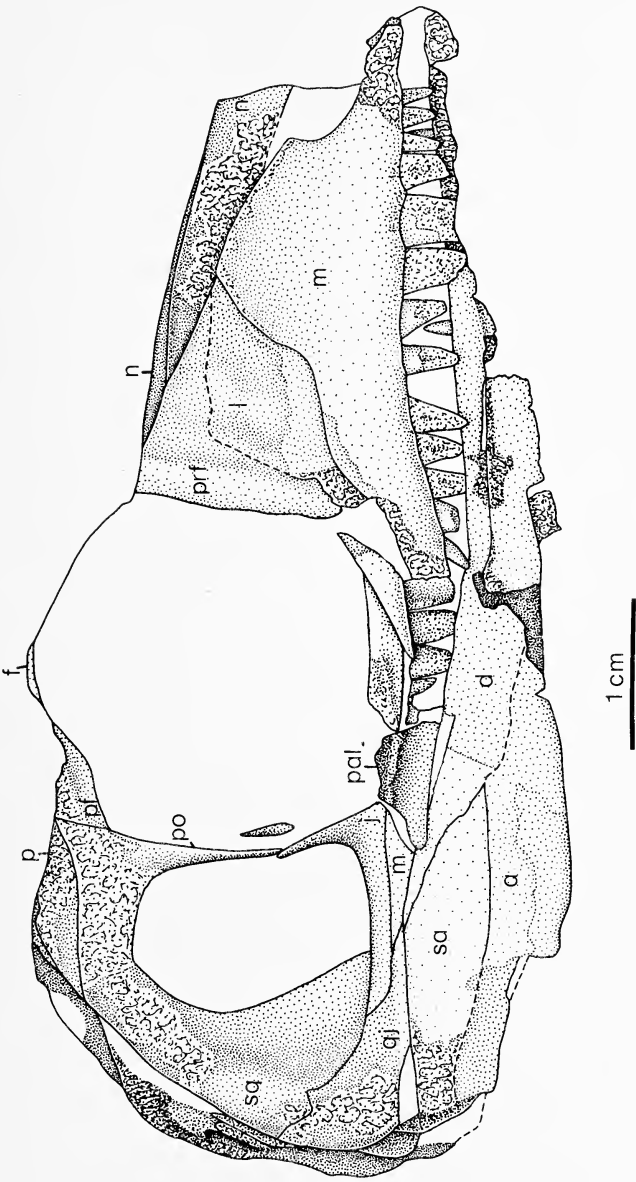


Fig. 4.—*Mycterosaurus longiceps*, holotype, FMNH-UC 692 as seen in Fig. 3.

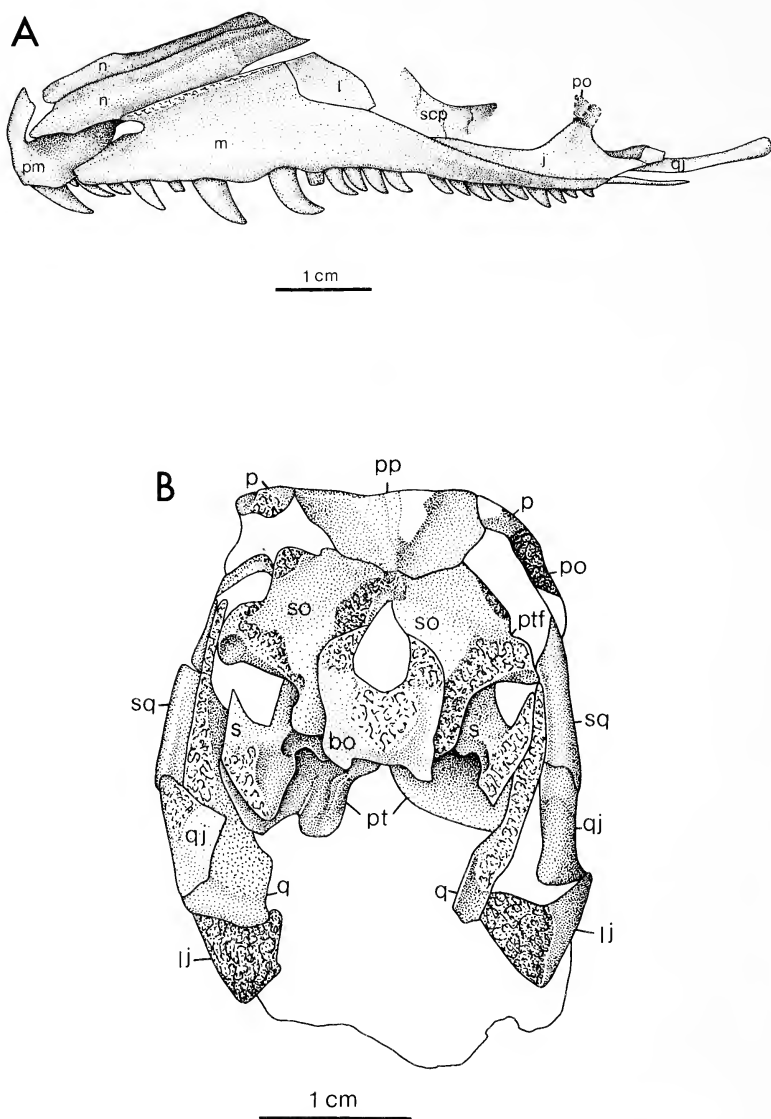


Fig. 5.—*Mycterosaurus longiceps*. A, anterior portion of skull AMNH 7002 in left lateral view, and B, occipital view of holotypic skull FMNH-UC 692.

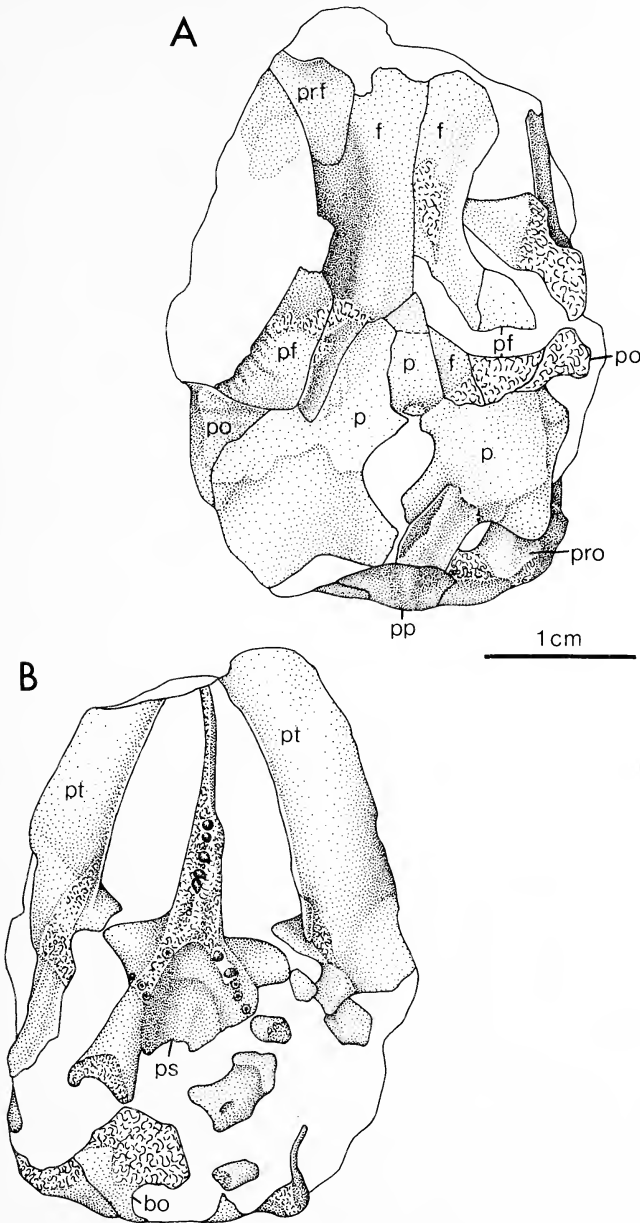


Fig. 6.—*Mycterosaurus longiceps*, FMNH-UC 169. A, dorsal, and B, ventral views of posterior portion of skull.

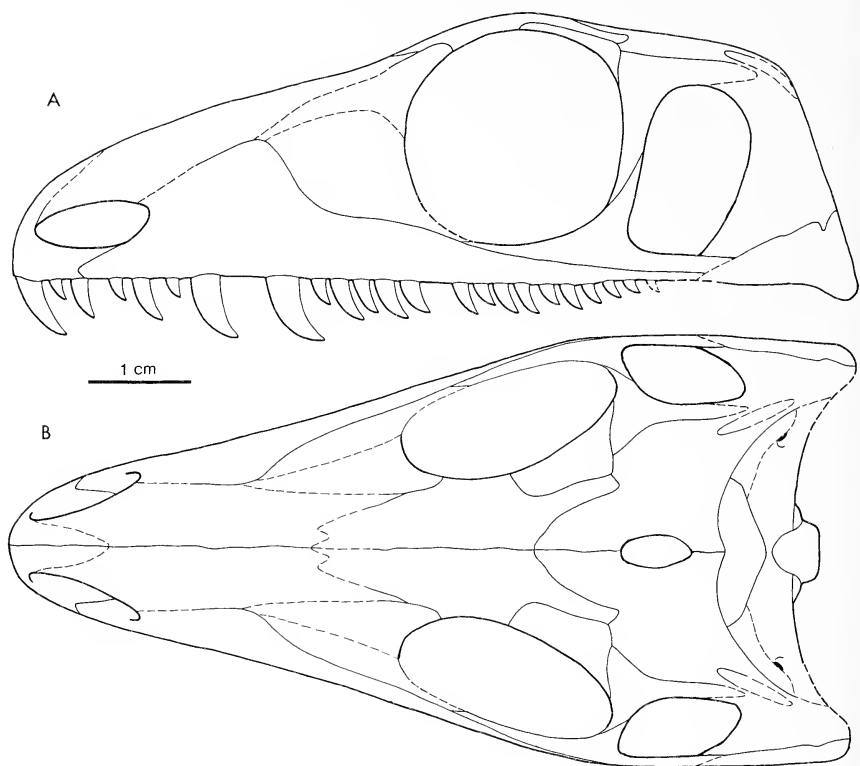


Fig. 7.—Reconstruction of skull of *Mycterosaurus longiceps* in A, lateral, and B, dorsal views.

largest of the premaxillary teeth is the first, about 6 mm in length, the second is in an early stage of replacement, and the third is about 4 mm in length. The first three maxillary teeth were probably subequal in length and about the same length as the third premaxillary tooth; maxillary teeth 4 through 9 are the largest of the series, reaching a maximum length of about 7 mm, whereas the remaining teeth decrease steadily in length posteriorly from slightly over 4 mm to just under 2 mm. There is no pronounced external swelling of the maxilla at the level of its largest teeth. Although the medial surface of the maxilla is not exposed, it can be assumed that there was no medial maxillary swelling above the largest teeth, as in spenacodontids, because the severe crushing in the holotype FMNH-UC 692 did not alter the external surface of the maxilla in this region. The tooth row ends posteriorly at the level of the postorbital bar.

The lacrimal is extremely broad dorsoventrally and probably formed much of the anterior orbital rim; its contribution to the anterior orbital margin cannot be defined precisely because it is represented mainly as impression. The lacrimal greatly overlapped the prefrontal and their internal suture is shown in Figs. 2 and 4 as a dashed line. It is not possible to determine the precise lengths of the nasals, frontals, and parietals because of their poorly preserved overlapping sutures. The frontal makes a moderate contribution to the dorsal orbital margin without a pronounced lateral extension. A narrow posterolateral process of the frontal is wedged between the postfrontal and parietal (Fig. 6A). The prefrontal appears to be a large element, but, as in the case of the lacrimal, is represented mainly as impression. The available evidence indicates that the prefrontal formed the anterodorsal margin of the orbit and had a long ventral process which extended along the medial surface of the orbital margin of the lacrimal. The expansive lacrimal restricts the prefrontal mainly to the dorsal surface of the skull roof. The postfrontal is almost entirely restricted to the dorsal surface of the skull. Its dorsal surface is lightly sculptured, whereas its lateral edge is rugose for attachment of orbital fascia. The broad parietal has a narrow anterior process along the midline; its posterior, occipital margin is broadly concave. The large, longitudinally oval parapineal foramen is near the posterior margin of the parietals. The postorbital, represented in both the holotype FMNH-UC 692 and FMNH-UC 169, is a large element. As preserved the postorbital does not project noticeably outward from the general plane of the lateral skull surface. There is, however, a low, sharp ridge on the postorbital that extends posterodorsally from the orbital rim to the dorsal margin of the temporal opening (Fig. 1). The basically triradiate jugal is excluded from the ventral margin of the skull by a maxillary-quadratojugal contact. Its dorsal process joins with the ventral process of the postorbital to form a narrow postorbital bar; the posterior process of the jugal has a wide contact with the squamosal at the posteroventral corner of the temporal fenestra that excludes the quadratojugal from the opening. The quadratojugal is essentially triangular in outline, expanding from its narrow anterior contact with the maxilla to the broad posterior portion that forms the posteroventral corner of the skull roof. The quadratojugal is wrapped around the posterior edge of the quadrate just above the condyle.

The occipital surface of the holotypic skull is poorly preserved (Fig. 5B). The tabulars and supratemporals are absent, much of the supraoccipital and opisthotics are damaged or missing, and the exoccipitals and basioccipital surfaces of articulation with the atlas-axis complex are broken off. The single postparietal appears to be paired in the holotype because of a broken median portion, clearly the result of

crushing; a single, median postparietal, restricted completely to the occiput, is present in AMNH 7002. At either end of the contact between the postparietal and supraoccipital is a deep, concave emargination; these openings were presumably covered by the missing tabulars. The lateral process of the supraoccipital and the paroccipital process of the opisthotic are incompletely preserved distally. These processes are separated by a small, shallow depression on the posterior surface of the occiput and a small notch that probably formed the medial border of the posttemporal fenestra.

Description of the palate and braincase in ventral view is limited to FMNH-UC 169, where only the parasphenoid, a small portion of the palate and fragments of the occiput are preserved. The parasphenoid is nearly complete but poorly preserved. It measures about 27 mm in length, of which the preserved portion of the cultriform process comprises about one-half. From a thin knife-like blade anteriorly, the process gradually increases in width posteriorly to the level of the basicranial articulation. The cultriform process bears a single row of well developed, pointed teeth. The parasphenoid is greatly expanded posterior to the basipterygoid processes into a broad, subtriangular plate. The lateral margins of the triangle are formed by a thick, convex ridge that supports a row of teeth like those on the cultriform process, but slightly larger. The distal half of the more complete right ventral ridge is marked with relatively coarse, longitudinal striations. Between these lateral ridges the ventral surface of the parasphenoid is deeply concave. The basipterygoid processes are triangular in outline with the free apex pointing laterally; the articular surface covers the anterior margin of the triangle. About all that remains of the palate are the pterygoids, which are represented mainly as impressions except in the area of the basicranial articulation. The greater part of the left epipterygoid is exposed in lateral view in the left orbit of the holotypic skull. In outline it is essentially a broad triangle with the dorsal apex continuing as a very long, splint-like process.

Both stapes are present in the holotype (Fig. 5B); the left is nearly complete, missing only the distal end of the columella, whereas the right is less complete, lacking that part of the columella distal to the anterior edge of the dorsal process. Both elements are preserved in place and are exposed only in occipital view. The footplate is extremely massive and has a very broad posterodorsal surface which meets a much narrower posteroventral surface in a sharp edge. The stapes is narrowest at the union of the footplate and columella. The columella extends posterolaterally and slightly ventrally from the footplate. In cross-section the shaft of the columella has the outline of a very narrow, inverted triangle; distally the vertical dimension of the

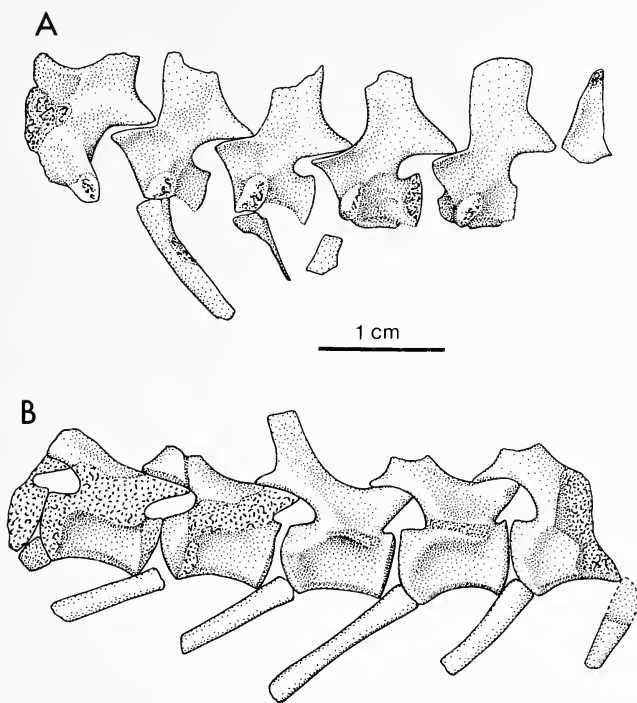


Fig. 8.—*Mycterosaurus longiceps*, FMNH-UC 169. A, left lateral view of vertebrae from region of cervical-dorsal transition, and B, right lateral view of anterior caudal vertebrae.

shaft increases greatly by ventral extension. Near its union with the footplate the posteromedial surface of the columella is pierced by the stapelial foramen. A flat, triangular dorsal process occupies a plane parallel with the long axis of the shaft. The apex of the dorsal process of the left stapes is well ossified and complete, with no indication of an articular surface for attachment to the otic region of the braincase. The dorsal process does not appear long enough to make contact with the braincase, even if allowance is made for distortion.

The lower jaws are preserved only in the holotype. Unfortunately, they are incomplete, poorly preserved, and very closely joined with the skull, allowing little comment about their structure. The jaw is apparently long and shallow, gradually reaching its greatest depth, though modest, at the level of the coronoid eminence. Posteriorly much of the external bone of the jaws has been lost and the sutures between the angular, surangular, and dentary are preserved mainly as internal

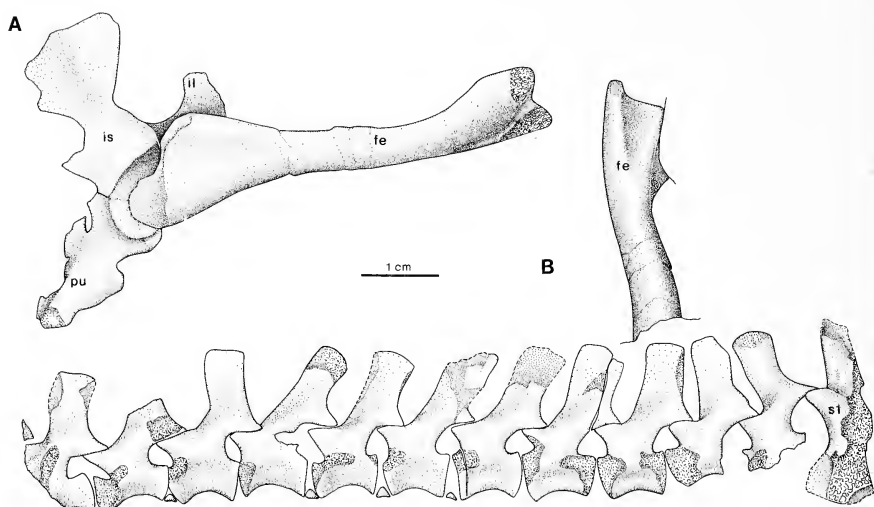


Fig. 9.—Portion of *Mycterosaurus longiceps* skeleton FMNH-UC 169 preserved in single nodule. A, right pelvis in lateral view and right femur in anterior view, and B, posteriormost 11 dorsal and first sacral vertebrae in lateral view, and right femur in posterior view (partly hidden from view by nodule).

impressions. The only notable feature is the unusually long dentary which extends as far posteriorly as does the maxilla. A few teeth of the lower jaw are partially exposed.

Vertebrae and ribs.—There are only three strings of vertebrae which can be adequately described and identified as to their location in the column, and also be safely attributed to *Mycterosaurus*. All three series are preserved in isolated nodules catalogued as FMNH-UC 169 (Figs. 8, 9B); it is not certain that they belong to a single individual.

A string of six vertebrae with fragments of closely associated ribs are preserved with the greater portion of a scapulocoracoid and a weathered proximal end of a humerus (Fig. 8A). These elements undoubtedly belong to a single individual and the vertebrae and ribs almost certainly include cervicals and anterior dorsals. The neural spines are rectangular blades in lateral view and their bases are slightly excavated just above the level of the zygapophyses. The zygapophyses are tilted only slightly downward and inward, and appear to extend slightly beyond the lateral surface of the centrum. There is no trace of a suture between the neural arch and centrum. The nearly vertical wing-like transverse process is complete only on the fifth vertebra of this series; it is positioned below the anterior zygapophysis and extends about 3 mm out from the surface of the centrum. From its thick-

er, dorsal edge the process shortens in length as it thins to a web of bone that extends anteroventrally to about the midheight of the anterior rim of the centrum. The lateral surface of the centrum is gently concave. The ventral surface of the centrum bears a poorly developed, rounded ridge that extends along the midline.

A second string of vertebrae comprises the posteriormost 11 dorsals and the first sacral; it is part of an articulated portion of skeleton that also includes the right pelvis, femur, and proximal ends of the tibia and fibula (Fig. 9). Although none of the posterior dorsals are complete, they do allow for a composite description except for the transverse process. Average measurements for the posterior dorsals are as follows: centrum length, 7 mm; centrum width, 7 mm; centrum height, 5 mm; spine height, 10 mm; total height, 20 mm. They differ only in minor ways from those of the cervical-dorsal region: the neural spines are relatively higher; the zygapophyses are tilted more steeply; the ventral surface of the centrum is less rounded in transverse section and there is no midline ridge; there is a slight ventral beveling of the ends of the centrum to accommodate the intercentra. In ventral view the intercentra are lozenge-shaped in outline; the narrowed lateral ends curve upward only very slightly. The first sacral vertebra is very incompletely preserved.

The third string of vertebrae includes nine caudals with haemal arches that probably come from the anterior region of the tail. Only the posterior five elements of this string are shown in Fig. 8B, and they have the following average measurements: centrum length, 8.5 mm; centrum height, 5.5 mm; spine height, 6 mm; total height, 14 mm. The narrow, short spine is positioned over the posterior end of the centrum; there is no sign of a lateral excavation of the neural arch or a suture between the neural arch and centrum. None of the transverse processes is preserved on the prepared side of the series; however, one process of the opposite side of the fifth vertebra of the series is exposed in a transverse break of the nodule. The process extends 7.5 mm laterally and slightly posteroventrally from the centrum, tapering in anteroposterior width distally from about 3 to 1 mm. The lateral surface of the centrum is deeply concave below the level of the transverse process. On either side of a very small longitudinal ridge on the midventral surface of the centrum is a closely paralleling ridge of equal size; the ridges become more pronounced posteriorly. Both ends of the centrum are beveled to accommodate the long, narrow haemal arches. Included among the AMNH 7002 material are many additional vertebrae of *Mycterosaurus*, most preserved in articulated strings; unfortunately, they are either poorly preserved, or their placement within the column is at best difficult to determine, or both.

The proximal ends of two ribs are preserved in position in the series

of vertebrae from the cervical-dorsal region of FMNH-UC 169. The holocephalous head is greatly expanded dorsoventrally so that it is triangular in outline; the head narrows distally from 6 mm to about 3 mm in a distance of 1 cm. The capitulum is a thin, triangular web that extends to the much thicker tuberculum, which is essentially a continuation of the shaft. The marked difference in thickness between the two heads is expressed only on the posteromedial surface of the rib; the opposite surface is flat. Although ribs are associated with the string of posterior dorsals of FMNH-UC 169, they are very poorly preserved. The first sacral rib is partially preserved on the left side. It shows the typical configuration of a narrow neck and an expanded blade-like distal portion that articulates with the ilium. There is no trace of a suture between the rib and vertebra.

Appendicular skeleton.—Four scapulocoracoids assignable to *Mycterosaurus* are preserved. A very poorly preserved right scapulocoracoid in the holotype is of little or no descriptive value. Three scapulocoracoids, a pair in AMNH 7002 (on separate blocks) and a right in FMNH-UC 169, are preserved in great part as impressions and lack essentially only part of the posterior coracoid (Fig. 10A, B); they are identical in details of their morphology. The anterior coracoid is greatly expanded anteriorly with a broadly convex anteroventral border. No suture can be seen between the scapula and coracoid, but in the scapulocoracoid of FMNH-UC 169 a small ridge that extends anterodorsally from the supraglenoid buttress across the lateral surface of the girdle to its anterior margin probably represents the original course of the suture. As is typical of pelycosaurs, just below this ridge there is a shallow, concave emargination in the anterior border of the anterior coracoid. There is no supraglenoid foramen in any of the specimens; in FMNH-UC 169 a large coracoid foramen is located beneath the anterior edge of the triangular supraglenoid buttress.

A fragment of the humerus representing part of the distal head is included in the holotype (FMNH-UC 692), a badly eroded proximal half of a right humerus is preserved with the scapulocoracoid of FMNH-UC 169 (Fig. 10B), and a partial left humerus, preserved as impression, is closely associated with the left scapulocoracoid of AMNH 7002 (Fig. 10A). They indicate that the humerus is a slim waisted and lightly constructed element with narrow proximal and distal ends. Although the supinator process is broken off, it certainly did not join the ectepicondyle to form an ectepicondylar foramen. No other elements of the forelimb or manus can be identified among the available materials as belonging to *Mycterosaurus*.

The pelvic girdle is represented only by the nearly complete right pelvis of the partial skeleton of FMNH-UC 169 (Fig. 9A). Although

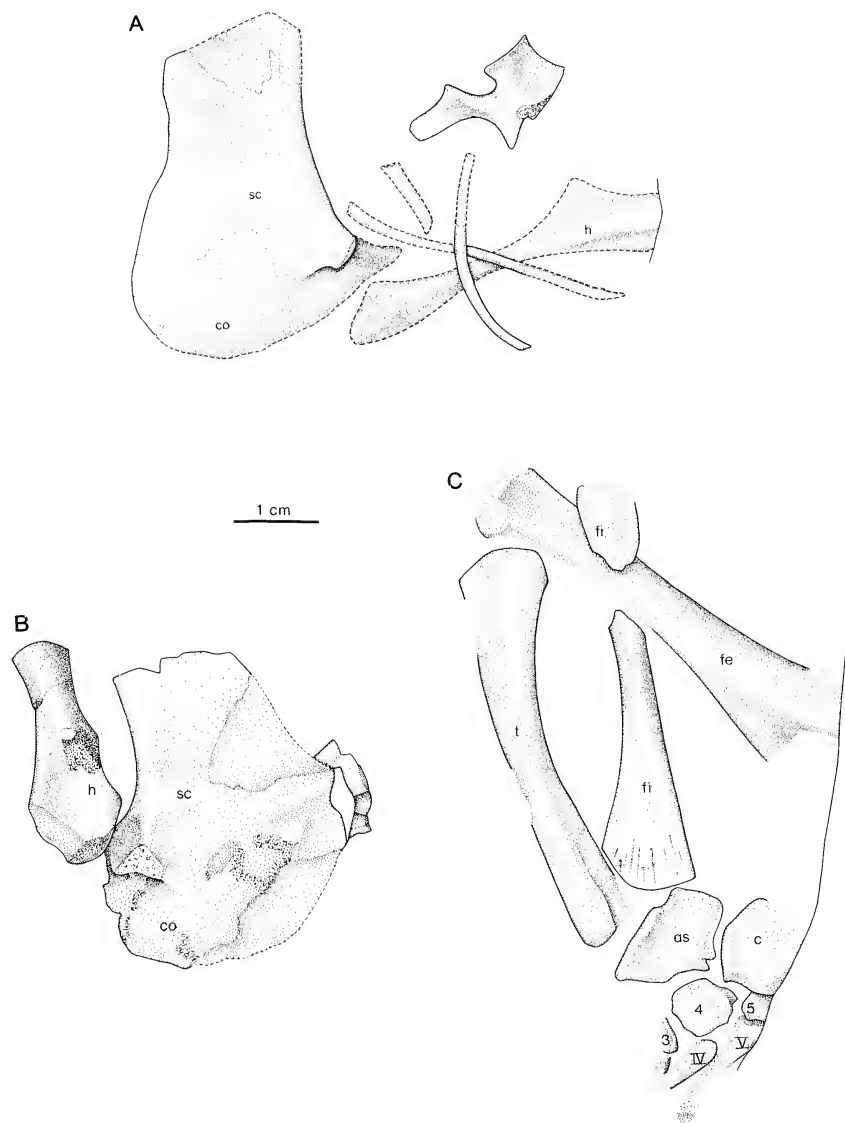


Fig. 10.—*Mycterosaurus longiceps*. A, left scapulocoracoid and humerus, vertebra, and rib fragments of AMNH 7002; B, partial right scapulocoracoid and proximal end of humerus of FMNH-UC 169; C, partial right limb and pes of AMNH 7002.

the iliac blade is represented mainly as impression, it is clear that it extended only posteriorly in varanopseid fashion and possessed a medial flange. The greatly thickened dorsal ridge of the pubis extends anteroventrally and laterally; at about its midlength it bears a massive lateral tubercle. Although the ventral plate of the pubis is incomplete, enough remains to indicate that it twists about the dorsal ridge from a near vertical projection posteriorly, facing only slightly ventrally, to a nearly medial projection anteriorly, facing posteroventrally and only slightly laterally. Ossification along the puboischadic suture is incomplete and there is a ventrally widening gap between the two elements; dorsally this gap reaches to within a few millimeters of the ventral lip of the acetabulum. It appears that this gap is at least in part the result of incomplete preservation of the pelvis. The horizontally elongate obturator foramen is located a short distance below the acetabulum and near the posterior border of the pubis; the posterior border of the foramen is incomplete. The ischium is incomplete ventrally. Its dorsal margin forms a slightly thickened, rounded ridge that extends with some tapering to the posteroventral corner of the element. In lateral view the dorsal ridge is straight for most of its length, turning upward slightly where it merges with the thickened area adjacent to the acetabulum.

Elements of the hindlimb identified as belonging to *Mycterosaurus* include: complete right femur with distal ends of the tibia and fibula of FMNH-UC 169 (Fig. 9); an incomplete, articulated left hindlimb and pes preserved as an impression on an isolated block of AMNH 7002 (Fig. 10C); an isolated proximal end of a left femur of the holotype. Description of the femur is based on that of FMNH-UC 169. The femur is long, about 58 mm, and slender. The anteroposterior width of the proximal end is about 24% of the length and that of the distal end is about 31%; at its narrowest point the shaft is subcircular in cross section and has a diameter of about 6 mm, about 10% of the length. In anterior view the dorsal outline of the femur has a gentle sigmoid flexure with the proximal end turned upward and the distal end downward, whereas the ventral outline is concave; this gives the distal end of the femur a decidedly downward curvature. In dorsal view the anterior margin is concave and the posterior margin is straight except for the widening at the distal end; this gives the femur a slight anterior curvature distally. The dorsal surface of the head is strongly convex with the anterior and posterior surfaces being nearly vertical; the ventral edges of these surfaces form the anterior and posterior boundaries of the short, yet deep, intertrochanteric fossa occupying the ventral surface of the head. The fossa is only about 14 mm long, occupying about 24% of the length of the femur. The smooth ridge bounding the anterior margin of the fossa extends much farther ven-

trally than the posterior limiting ridge. Further, it gradually expands ventrally as it extends proximally nearly to the end of the femur. The anterior limiting ridge terminates proximally as a straight, thin edge whose unfinished surface is continuous with the anteroventral margin of the articular surface of the head. There is no distinct internal trochanter along the anterior limiting ridge. Typically in pelycosaurs the distal or central portion of the anterior limiting ridge supports a prominent internal trochanter which is connected to the anteroventral corner of the head by a much reduced, curved ridge (Romer and Price, 1940). The femur of *Mycterosaurus* also exhibits no signs of an adductor crest or fourth trochanter; if present at all, they were only very weakly developed. On the dorsal surface the long, narrow intercondylar fossa extends about 12 mm onto the distal end of the shaft; as expected the posterior condyle is slightly longer than the anterior. The ventral popliteal area is a smooth, broadly concave depression.

The left tibia and fibula of AMNH 7002 (Fig. 10C) are about the same length, 47 and 46 mm respectively, and are roughly 78% of the estimated length of 60 mm for the incomplete femur associated with them. The tibia is incompletely exposed dorsolaterally; the lateral margin is slightly concave and the entire element is arched slightly dorsally. The dorsally exposed fibula is nearly complete, missing only a small section of the shaft near the proximal end. The mediolateral width of the proximal end is about 15% of the length and that of the distal end is about 24%; the shaft is about 4 mm in mediolateral width at its narrowest point, or about 9% of the length. The lateral margin is essentially straight, whereas the medial margin is broadly concave due mainly to the medial flaring of the distal end.

The partial pes of AMNH 7002 is exposed in dorsal view and includes the astragalus, calcaneum, distal tarsals 3, 4, and 5, and metatarsals 4 and 5. The astragalus is complete; its dorsal surface is moderately concave. The mediolateral width is about 70% of the proximodistal length. The tibial facet of the astragalus occupies about 75% of the distal length of the medial border; proximal to the tibial facet the medial border retreats laterally about 1 mm. The distal end of the lateral border opposing the calcaneum is drawn out into a small projection that forms a notch-like medial border of the perforating foramen. Just distal to the perforating foramen the laterodistal corner of the astragalus has a deep, slightly concave emargination for contact with the fourth distal tarsal. The lateral border of the calcaneum is not complete, but was undoubtedly broadly convex in typical pelycosaur fashion. The dorsal surface of the calcaneum is nearly flat. The contribution of the calcaneum to the perforating foramen is not as pronounced as that of the astragalus. The fourth distal tarsal is pentagonal in outline with major contacts with the astragalus, calcaneum, and

fourth metatarsal. Short, slightly concave lateral and distomedial facets contact the fifth and third distal tarsals respectively, and there is a distinct, straight, medial margin that undoubtedly contacted the missing medial centrale.

SYSTEMATIC RELATIONSHIPS OF *MYCTEROSAURUS LONGICEPS*

Rejection of Romer and Price's Assessment

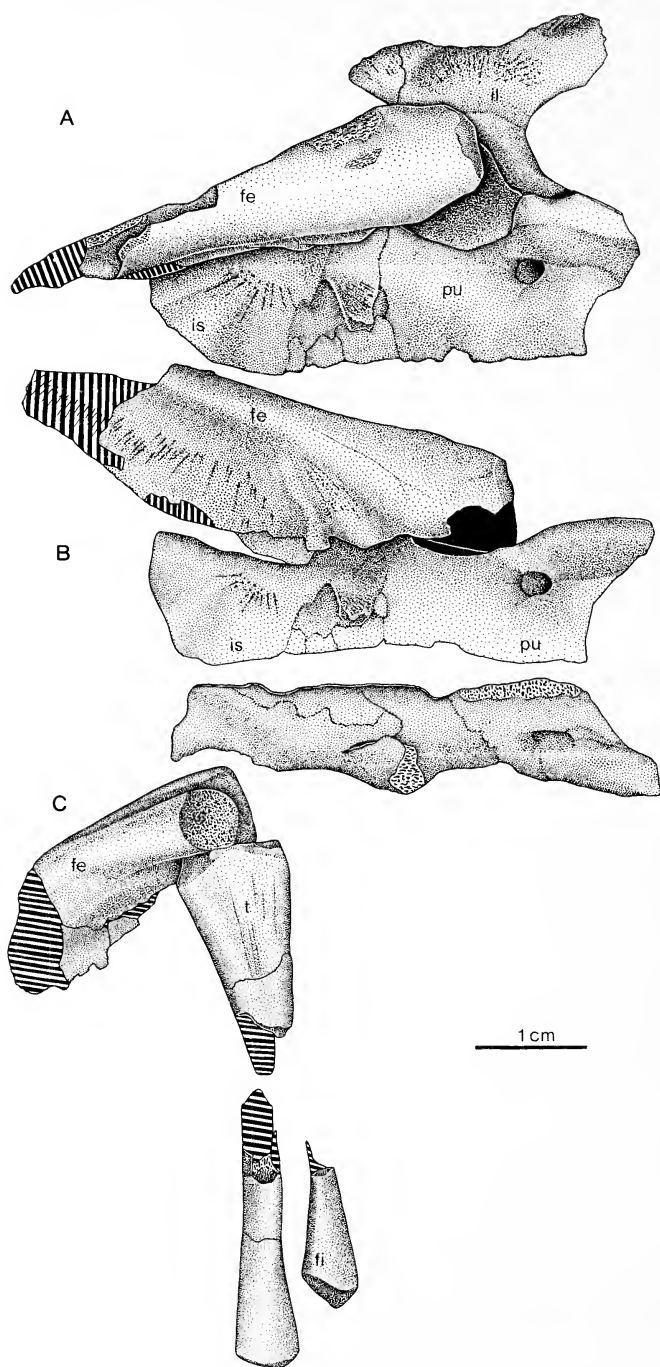
Romer and Price (1940) erected the family Nitosauridae to include *Mycterosaurus longiceps* and *Nitosaurus jacksonorum*. Nitosauridae was grouped with the families Edaphosauridae, Lupeosauridae, and Caseidae within the suborder Edaphosauria. The Nitosauridae was judged by Romer and Price (1940) as a primitive family of the suborder and close to the ancestry of the caseids. Restudy by Reisz (1980) of the known material of *N. jacksonorum* from the Lower Permian Cutler Formation of New Mexico has revealed that the diagnosis of this species is based on poorly preserved and unassociated elements that may belong to two different types of pelycosaurs. Furthermore, there is no basis for associating *Mycterosaurus* with *Nitosaurus* within a single family. Reisz (1980) has also argued that the family Lupeosauridae, established by Romer and Price (1940) to include *Lupeosaurus kayi*, is an invalid taxon. The inclusion of the Caseidae within the suborder Edaphosauria has also been seriously questioned. On the other hand, a close relationship between the caseids and the eothyridids of the suborder Ophiacodontia was recognized by Vaughn (1958) and Langston (1965), and the latter further suggested that the caseids and edaphosaurids be placed in separate suborders. Reisz (1980) not only concurred with this position, but in an analysis of the phylogenetic relationships of the major pelycosaurian groups concluded that the caseids and eothyridids form a sister group to the other pelycosaurian families, including the Edaphosauridae. However, in a detailed study of the family Caseidae, Olson (1968) expressed some reservations on the relationships suggested by Vaughn (1958) and Langston (1965).

Romer and Price (1940) were undoubtedly correct in attributing all of the *Mycterosaurus longiceps* specimens to the Mitchell Creek nodular deposit of the Clyde Formation of Texas. It is important to point out, however, that the specimens were preserved in several nodules, each containing only a portion, or portions, of the skeleton. The nodules weathered out of a clay-shale deposit and were discovered lying well isolated from one another over a considerable area. Although examination of all the materials assigned to *M. longiceps* reveals that most can be safely referred to that species, at least one other taxon, possibly more, has been mistakenly associated with this species. This led to serious errors in the description and systematic assessment of

M. longiceps by Romer and Price. Nearly all of the features noted by Romer and Price as indicating that *M. longiceps* is an edaphosaur antecedent to the caseids were based on the postcranial skeleton; they viewed the skull as indicating nothing more than a primitive pelycosaurian grade of development. Most of the significant diagnostic features used by Romer and Price were based on an articulated portion of skeleton that probably belongs to a temnospondylous amphibian, possibly a dissorophid. This specimen, mistakenly included among the *M. longiceps* materials of FMNH-UC 169, contains the pelvis, partial hindlimb, and fragments of the sacral vertebrae (Fig. 11). The incorrectness of this erroneous association is strongly suggested by the presence of another articulated portion of skeleton (Fig. 9), bearing the same catalog number, that includes a string of 11 dorsal and at least one sacral vertebrae, pelvis, and femur of a lightly built pelycosaur. This specimen is not only the same size as FMNH-UC 692 (holotype), AMNH 7002, and the other portions of FMNH-UC 169, but the vertebrae and femur are identical to those included among these specimens and are typically pelycosaurian in structure.

A variety of vertebrates have been identified in the same Mitchell Creek nodular deposit that produced the *Mycterosaurs* specimens. These include the microsaure *Pantylus cordatus*, the dissorophid amphibian *Broiliellus*, the captorhinomorph reptile *Eocaptorhinus laticeps*, and the pelycosaur *Glacosaure megalops*. Of particular concern among these forms is *G. megalops*, which is known only by a single skull that is about one-half the length of *M. longiceps*. Romer and Price (1940) suggested that some of the postcranial materials assigned to *M. longiceps* may actually belong to *G. megalops*, considered by them to be an edaphosaur probably representing a type transitional between the longer-faced nitosaurids and the short-snouted caseids. Lewis and Vaughn (1965) have also recognized the possibility of such a confusion, noting that the association of the skull of *G. megalops* with the disproportionately larger postcranial skeleton in the reconstruction of *M. longiceps* by Romer and Price (1940) would produce a small-headed form, a feature characteristic of the caseids.

The partial postcranial skeleton probably pertaining to a temnospondylous amphibian which was mistakenly included among the *M. longiceps* materials FMNH-UC 169 and which Romer and Price (1940) relied so heavily on in their analysis of the systematic relationships of *M. longiceps* is shown in Fig. 11. In particular, they noted that the remarkably long anterior expansion of the iliac blade is seen only in caseids and the well developed adductor crest of the femur is characteristic of edaphosaurs in general. As the above description indicates, neither of these features is found in *M. longiceps*. Other comparisons made by Romer and Price seem equally invalid. They described



M. longiceps as having a humerus with a remarkably narrow head and an astragalus with a long neck, noting that the former feature is found only in caseids, whereas the latter is very typical of edaphosaurs. A humerus with a narrow proximal head is not characteristic of all caseids and is also not exclusive to caseids (Olson, 1968). Even if the humerus was relatively slender, it should not be too unexpected in light of the slender build of the hindlimb. The one astragalus that can be confidently assigned to *M. longiceps* has a decidedly short neck. The one feature noted by Romer and Price that would appear to link *M. longiceps* with the caseids is the absence of a supraglenoid foramen. They also noted the absence of the foramen in *Nitosaurus jacksonorum*, but examination of the type material does not substantiate this statement. Further, Langston (1965) has described a scapulocoracoid possibly belonging to *Oedaleops* that also lacks this foramen. The absence of a supraglenoid foramen in *Oedaleops* is not unexpected in view of the fact that the eothyridids and caseids are considered very closely related (Langston, 1965; Reisz, 1980). The somewhat greater than normal anterior expansion of the anterior coracoid in *M. longiceps* that is also seen in edaphosaurs in general need not be judged a sign of relationship, as Romer and Price did, but as the retention of a primitive feature. Romer and Price also cited the absence of lateral excavations of the vertebral neural arches and a longitudinal ventral keel of the centra as features relating *M. longiceps* to the caseids and edaphosaurs. The absence of these features, which are normally well developed in advanced sphenacodontids, is here interpreted as a primitive state and, therefore, not as a sign of relationship (Reisz, 1980). There is, however, at least incipient development of lateral excavations of the neural arches of the dorsal vertebrae in *M. longiceps*. The slender, long, hindlimb elements of *M. longiceps* are certainly more characteristic of carnivorous varanopseids, or even sphenacodontids, than of caseids or edaphosaurids. With the exception of the specialized feature of lacking a supraglenoid foramen, *M. longiceps* possesses no other features that would suggest a connection with either the Edaphosauridae, believed by some to be the only valid family of the Edaphosauria, or the Caseidae, which, with the Eothyrididae, may constitute a separate suborder.

Lewis and Vaughn (1965) described a second species of *Myctero-*

←

Fig. 11.—Probable temnospondylous amphibian pelvis and right hindlimb mistakenly described by Romer and Price (1940) as part of *Mycterosaurus longiceps* FMNH-UC 169. A, pelvis in lateral and proximal end of femur in dorsal view; B, pelvis in ventral and proximal end of femur in anterior view; C, disassociated distal end of femur in posterior view, and tibia and distal end of fibula in dorsal view.

saurus, *M. smithae*. Unfortunately, neither the holotype (MCZ 2985), consisting of the greater part of a skull and partial postcranial skeleton, nor some referred postcranial material (USNM 22098) confirm or deny any of the postcranial evidence presented by Romer and Price (1940) to argue that *M. longiceps* is an edaphosaur close to the ancestry of the caseids.

Mycterosaurus longiceps as a Primitive Varanopseid

In contrast to the view held by Romer and Price (1940), the skull, rather than the postcranial skeleton, is here considered the key to the systematic position of *Mycterosaurus longiceps*; on this basis *M. longiceps* is placed in the family Varanopseidae. Close comparisons with other varanopseids are limited to three genera, containing four species, that more or less follow one another in time from the Early to the early Late Permian—*Aerosaurus greenleeorum* Romer (1937) and *A. wellesi* Langston and Reisz (1980) from the Wolfcampian (earliest Permian) Cutler Formation of north-central New Mexico; *Varanops brevirostris* (Williston, 1911) from the Leonardian (later Early Permian) Vale Formation of north-central Texas (Romer and Price, 1940); *Varanodon agilis* Olson (1965) from the Guadalupian (earliest Late Permian) Chichasha Formation of central Oklahoma. All but *A. greenleeorum* are based on complete or nearly complete specimens. Several poorly known Permian and Pennsylvanian forms have been tentatively regarded as varanopseids, but a recent reappraisal by Langston and Reisz (1981) of these assessments indicates that they should remain tentative.

The most obvious and important feature linking *M. longiceps* to the varanopseids is the great posterior extension of the maxilla to a level beyond the postorbital bar where it contacts the quadratojugal of normal length. Among the pelycosaur only the eothyridids *Eothyris* and *Oedaleops* are known to have a maxillary-quadratojugal contact. In contrast to the varanopseids, however, it is achieved by an unusually long quadratojugal contacting a maxilla of standard length. The great posterior extension of the maxillary dentition is also apparently unique to the varanopseids. In *M. longiceps* the maxillary tooth row ends just beyond the level of the postorbital bar as in *Aerosaurus*, whereas in *Varanops* and *Varanodon* it extends somewhat farther. In *M. longiceps* and the other three varanopseid genera the frontal makes a moderate entrance into the orbital rim without development of a lateral process. Well developed parasphenoidal teeth are present in *Aerosaurus*, *Varanops* and *M. longiceps*; however, they are far more extensively developed in *Aerosaurus*. It is not known whether this feature is present in *Varanodon*.

Common to the varanopseids is the very large lateral temporal fe-

neustra which reduces the ventral arch to a thin bar. Although the temporal fenestra of *M. longiceps* is not as greatly expanded posteroven- trally as is otherwise standard in varanopseids, it is as fully developed along its other margins and does restrict the anterior end of the ventral arch to a thin bar. The relative height of the temporal fenestra in *M. longiceps* is comparable to those of *Aerosaurus* and *Varanops*, and is considerably greater than that of *Varanodon* (Table 1). Also typical of the varanopseids is the thin postorbital and suborbital bars. In *M. longiceps* and *Aerosaurus* both bars are very thin; in *Varanops* and *Varanodon* the postorbital bar is somewhat wider, whereas the sub- orbital bar is considerably wider. The upper marginal dentition of *M. longiceps* is nearly identical to that of *Aerosaurus* in the number of premaxillary and maxillary teeth, tooth shape, and pattern of enlarge- ment. In *Varanodon* the teeth of the upper jaw are more numerous, but their shape is similar to those of *M. longiceps* and *Aerosaurus*. *Varanops* has the same number of teeth on the upper jaw (33) as *Varanodon*, but the known skulls are so badly damaged that the exact shape of the teeth cannot be determined. In *Mycterosaurus*, *Aerosau- rus*, and *Varanops* the jugal-lacrimal contact is narrow and simple, whereas in *Varanodon* it is not only broader, but is strengthened by a sinuous suture. Probably related to this feature is the increased wid- ening of the suborbital bar in the varanopseids.

It appears that the dorsal process of the stapes of *M. longiceps* did not make direct contact with the otic region of the braincase. A similar conclusion was made by Langston and Reisz (1981) about *Aerosaurus wellesi*. They noted that the proximal part of the anteroventral surface of the paroccipital process of *A. wellesi* is smooth and gently convex, and lacks the long massive ridge for the attachment of the dorsal pro- cess of the stapes which is typical of spenacodonts and edaphosaurs. Among pelycosaurs only in *Mycterosaurus* and *Aerosaurus* is the basi- cranial process triangular in ventral view. This structure has not been described in either *Varanops* or *Varanodon*.

The above comparisons demonstrate that *M. longiceps* is best con- sidered a member of the Varanopseidae. Further, on the basis of cra- nial anatomy it appears that *M. longiceps* not only compares more closely with *Aerosaurus* than with *Varanops* or *Varanodon*, but that the series *Aerosaurus*, *Varanops*, and *Varanodon* exhibits an increas- ing departure from *M. longiceps*. These observations are most rea- sonably explained by the fact that *M. longiceps* and *Aerosaurus* are nearly contemporaneous and occur considerably earlier than *Varanops* and *Varanodon*. The progressive increase in differences between *M. longiceps* and the consecutively occurring *Aerosaurus*, *Varanops*, and *Varanodon* are probably due, at least in part, to morphological trends within the Varanopseidae. If it is accepted that *M. longiceps* repre-

Table 1.—Skull proportions relating to temporal fenestra of varanopseids. Abbreviations: PSL, postorbital skull length; SL, skull length; TFH, temporal fenestra height; TFL, temporal fenestra length. Measurements for *V. agilis*, *V. brevirostrus*, and *A. wellsi* based on restorations by Olson (1965), Romer and Price (1940), and Langston and Reisz (1980), respectively.

Species	TFH/TFL	TFL/SL	TFH/SL	PSL/SL
<i>Varanodon agilis</i>	.38	.31	.12	.41
<i>Varanops brevirostrus</i>	.60	.27	.16	.36
<i>Aerosaurus wellsi</i>	.79	.26	.20	.33
<i>Mycterosaurus longiceps</i>	1.45	.14	.20	.28

sents in general the most primitive grade of organization within the Varanopseidae, then some of the more striking differences between its skull and those of the other varanopseids can be accounted for. The smaller size of the temporal fenestra in *M. longiceps*, in particular the posteroventral region, can only be interpreted as a primitive feature. It is also reasonable to speculate that posteroventral enlargement of the temporal fenestra of *M. longiceps* would result in concomitant changes of the skull that would bring it into closer accord with those of the other varanopseids. These changes would include a reduction in the size of the squamosal and quadratojugal, loss of the subtemporal process of the squamosal that contacts the jugal, and a greater thinning of the subtemporal bar. In the series *Aerosaurus*, *Varanops*, and *Varanodon* there is a progressive lengthening of the postorbital portion of the skull, posterior positioning of the jaw point, and a lengthening and lowering of the temporal fenestra (Table 1). The position of the jaw joint in *M. longiceps* is typical among pelycosaur, lying at about the level of the occipital condyle, whereas in *Aerosaurus* it is somewhat posterior to the condyle. Although there is a considerable lengthening of the temporal opening in *Aerosaurus* over that of *M. longiceps*, the relative heights of the fenestra of both genera are similar. In *Varanodon*, where these trends reach an extreme, half the length of the postorbital region of the skull, as well as the temporal fenestra, extends posterior to the occipital condyle. Within the varanopseids there has been a strengthening of the postorbital bar through gradual widening of this strut-like structure. Further, in *Varanodon* there is an anterior expansion of the squamosal above the temporal opening that not only results in a reduction in the height of the opening, but also in a narrow contact between the squamosal and jugal. This feature is not seen in any other pelycosaur.

M. longiceps also exhibits several features of the postcranial skeleton which indicates a primitive level of organization within the Varanopseidae. With the exception of slightly shorter neural spines, the

general proportions of the dorsal vertebrae of *M. longiceps* are similar to those of *Aerosaurus*. Langston and Reisz (1981) noted that the spines of the immature *A. wellesi* specimens studied by them are significantly shorter than those of the immature and only known specimens of *Varanops*. In *Varanodon* there appears to be at least a small, relative increase in spine height over that of *Varanops*. Relative increase in spine height is a common trend among the pelycosaurs. The incipient development of the lateral excavations of the neural arches of *M. longiceps* can only be viewed as primitive relative to other varanopseids. Excavation of the neural arches in *Aerosaurus* and *Varanops* is less pronounced than in the sphenacodonts (Langston and Reisz, 1981). The presence or absence of excavated neural arches in *Varanodon* is not mentioned by Olson (1965). The absence of a well developed mid-ventral, longitudinal keel of the dorsal centra in *M. longiceps* is also interpreted as primitive for the varanopseids. The middorsal centra of *A. wellesi* are described by Langston and Reisz (1981) as having a well developed keel that is less pronounced than that of *Varanops* or sphenacodonts. The possession of single-headed dorsal ribs sets *M. longiceps* apart as more primitive than the other varanopseids, whose ribs are double headed. The contact between the astragalus and the fourth distal tarsal is primitively very broad in *M. longiceps*, whereas in *Aerosaurus* and *Varanops* it is greatly reduced; the pes of *Varanodon* is unknown. The possession of a massive lateral tubercle of the pubis in *Mycterosaurus* is a primitive feature not seen in other varanopseids.

Whereas *M. longiceps* possesses a great number of features which indicate a very primitive position within the Varanopseidae, it also exhibits several important specialized features otherwise not seen in the family. Most striking is the great development of the dorsal lamina of the maxilla that not only excludes the lacrimal from the naris, but also greatly shortens its length; a similar condition is seen only in advanced sphenacodontids. The lack of a supraglenoid foramen is viewed as a specialized feature. The absence of the internal and fourth trochanters and adductor crest, as well as the extension of the anterior limiting ridge of the intertrochanteric fossa proximally without break nearly to the end of the femur is a combination of features not seen in any other pelycosaur. These features in *M. longiceps* are an early, wide divergence from the general structural trends of the varanopseids. This suggests that *Mycterosaurus* may represent a distinct lineage divergent from the evolutionary line, or closely paralleling lines, that includes the other varanopseids.

Comparison with Mycterosaurus smithae

The only other described species of *Mycterosaurus*, *M. smithae* Lewis and Vaughn (1965), is from the Lower Permian Cutler Formation of southwestern Colorado. The holotype (MCZ 2985) is a poorly

preserved specimen consisting of a partial skull, five vertebrae with ribs, and fragments of limbs and other elements; a referred specimen (USNM 22098) from the same formation and area includes seven or more poorly preserved, articulated posterior dorsal vertebrae, a partial left femur, and fragments. Generic assignment of *M. smithae* was based primarily on the following features: similar size and proportions of the skull and postcranial elements to those of *M. longiceps*; temporal fenestra greatly expanded vertically; entrance of the maxilla into the orbit to prevent a lacrimal-jugal contact. Assignment to *Mycterosaurus* also seems to have been arrived at in part as a process of elimination of all other known pelycosaur genera of comparable size.

In view of the fact that *M. smithae* specimens do not exhibit any of the important diagnostic characters of either Varanopseidae or *Mycterosaurus*, its assignment to either taxon should be considered provisional. If, however, *M. smithae* is correctly assigned *Mycterosaurus*, then the specific diagnosis given by Lewis and Vaughn (1965, p. 34–35) clearly indicates, as they concluded, that it is more primitive than *M. longiceps*: “. . . temporal fenestra of only three-tenths as much area as that in *M. longiceps*; zygomatic arch more than twice as deep, and distance from posterior border of temporal fenestra to posterior border of squamosal about one and one-half times as long as in *M. longiceps*; largest maxillary teeth about two-thirds as thick at base as in *M. longiceps*.” Lewis and Vaughn (1965) assessed the age of the large Cutler Formation faunal assemblage of Colorado described by them, of which *M. smithae* is a member, as equivalent to that of the lower and middle parts of the Wichita Group of Texas. On this basis *M. smithae* occurs somewhat earlier than *M. longiceps* and is approximately the same age as *Aerosaurus*.

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A RECORD OF *RHINOLOPHUS ARCUATUS* (CHIROPTERA: RHINOLOPHIDAE) FROM NEW GUINEA, WITH THE DESCRIPTION OF A NEW SUBSPECIES

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ABSTRACT

The Indo-Australian species of *Rhinolophus* currently referred to the *R. arcuatus* group are keyed and listed, with the description of a new subspecies of *R. arcuatus* from New Guinea, whence the species has not hitherto been recorded. Three species of the genus, *R. megaphyllus*, *R. euryotis*, and *R. arcuatus* are now known from New Guinea or the nearby islands, and comparative notes are provided.

INTRODUCTION

Among the numerous species of Indo-Australian bats of the genus *Rhinolophus* only *R. megaphyllus* and *R. euryotis* have been reported from New Guinea or from the islands immediately nearby, although on distributional grounds it is possible that the widespread species *R. philippinensis* may also occur there. Two species, *R. megaphyllus* and *R. philippinensis*, are known to occur in Australia but the genus is unknown from the Solomon Islands, the New Hebrides, or from any of the Pacific islands further to the east. It seems clear that Australia,

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with New Guinea and some of its more closely associated islands such as those of the Bismarck Archipelago (Koopman, 1979) to the north-east or the Louisiade Archipelago immediately to the east, may mark the eastward extension of this widely distributed Old World genus, especially when their apparently rather sparse rhinolophid fauna is compared with the profusion of species that occur in the Malaysian region to the west. The discovery of a third species, *R. arcuatus*, in New Guinea therefore has both faunal and zoogeographic interest, perhaps the more so because its representative in New Guinea seems more closely allied to those from the Philippine Islands, Borneo, and Sumatra than to those from the geographically nearer Molucca Islands.

Two of the six groups of *Rhinolophus* recognized by Andersen (1905b, 1918) and, in the Orient, of the four delimited by Tate and Archbold (1939) thus occur in New Guinea, with *R. megaphyllus* representing the *ferrumequinum* (= *simplex* or *megaphyllus*) group, and *R. euryotis* and *R. arcuatus* the *arcuatus* (= *euryotis*) group. Numerous representatives of both groups occur elsewhere to the west, the *ferrumequinum* complex extending to the Palaearctic and Ethiopian regions, the *arcuatus* group to the Philippine Islands and to the southeast Asian mainland. The *philippinensis* (= *luctus*) group (including the *macrotis* group of Andersen, 1905b) has a predominantly Oriental and African distribution. It is represented in the eastern part of the Indo-Australian region by *R. philippinensis* in Sulawesi, Timor (Goodwin, 1979), and in Queensland, Australia, a pattern suggesting that in time it may be found in New Guinea. No member of the *pusillus* (= *minor* or *lepidus*) group has been reported east of Borneo and the more westerly (Lombok) of the Lesser Sunda Islands, although like the *ferrumequinum* group it extends to the Palaearctic and Ethiopian regions. The *midas* group of Andersen (1905b) is primarily Palaearctic but just extends into Africa; the *macrotis* group as defined by the senior author is found in both Africa and the Orient but in the east does not extend beyond the Philippine Islands, Malaya, and Sumatra. Tate (1943) incorporated this last group into the *philippinensis* complex, with which its members closely agree.

SYSTEMATICS

Members of the *arcuatus* group of *Rhinolophus* are characterized by large, broad ears with well developed rectangular antitragal lobe; a large, wide noseleaf that covers the muzzle; an expanded internarial septum; a large, usually ovate or sub-ovate sella; the skull with high, projecting median anterior rostral swellings and short palatal bridge; its length one-third to one-quarter the length of the maxillary toothrow; dentally, the small anterior upper premolar (PM2) remains in the toothrow; the second lower premolar (pm3) being very small and extruded.

They differ from the members of the *philippinensis* group chiefly in the presence of a high connecting process and in the very short palatal bridge; however, *R. macrotis* of the *philippinensis* group has a higher process than most of the associated species but has a very long palate, and in the *arcuatus* group, *R. creaghi* and *R. canuti* lack any real connecting process, which in these is replaced by a tuft of hairs. The *arcuatus* group also overlaps in the Moluccas and New Guinea with members of the *ferrumequinum* group, but in these the ears and antitragus are not greatly enlarged, the internarial septum little expanded, and the facial part of the skull is long with the median rostral swellings not especially high and projecting. All have a rounded connecting process but it originates on the back of the sella from a point below the tip, rather than from the apex of the sella as is more usual in the *arcuatus* group.

The *Rhinolophus arcuatus* group was briefly reviewed and characterized by Andersen (1905a) and its species and subspecies listed by Tate and Archbold (1939). The several species currently referred to it may be keyed:

1. Anterior leaf narrowly emarginated, the emargination prolonged posteriorly as a narrow, linear groove on face of leaf, extending less than halfway to internarial region 2
- Anterior leaf scarcely emarginated, but with broad, parallel swollen longitudinal ridges extending from edge of leaf to internarial region, enclosing a groove that widens posteriorly to terminate at a low, median projection *euryotis*
2. Connecting process low or obsolete; lower part of posterior leaf densely pilose 3
- Connecting process evident; lower part of posterior leaf, at most, sparsely haired 4
3. Upper part of sella thickened posteriorly; connecting process obsolete; hairs at base of posterior leaf forming a dense, bristly sub-conical tuft *creaghi*
- Upper part of sella lacking any posterior thickening; connecting process low, rounded; hairs at base of posterior leaf long, dispersed *canuti*
4. Posterior leaf thickened and folded to form a vertical fissure enclosing rear of connecting process 5
- Rear of connecting process attached directly to face of posterior leaf, not enclosed 6
5. Postnarial rostral depression prominent, moderately deep, elongate, enclosed by broad, well developed supraorbital ridges *coelophyllus*
- Postnarial rostral depression shallow, short, little developed; supraorbital ridges narrow *shameli*
6. Upper part of sella unmodified 7
- Upper part of sella forming a small, triangular pouch, its opening directed downwards *inops*
7. Size small to moderate, length of forearm not exceeding 60 mm 8
- Large, length of forearm 66–71 mm *rufus*
8. Larger, length of forearm 53–57 mm, maxillary tooththrow 9.5–10.4 mm; internarial cup narrow; prominent frontal depression *subrufus*
- Smaller, length of forearm 42–51 mm, maxillary tooththrow 7.8–8.6 mm; internarial cup expanded; shallow frontal depression *arcuatus*

Subspecies, where appropriate, and distributions are:

Rhinolophus euryotis euryotis Temminck, 1834

Ambon I, Ceram I, Timor Laut I, Molucca Is; Sulawesi (The Sulawesi population is currently under description by the senior author as a distinct subspecies.)

Rhinolophus euryotis timidus Andersen, 1905a

Batchian I, North Molucca Is; New Guinea; Bismarck Is (Smith and Hood, 1981)

Rhinolophus euryotis praestans Andersen, 1905a

Kei Is

Rhinolophus euryotis aruensis Andersen, 1907a

Aru Is

Rhinolophus euryotis burius Hinton, 1925

Buru I, Molucca Is

Rhinolophus creaghi creaghi Thomas, 1896

Borneo

Rhinolophus creaghi pilosus Andersen, 1918

Madura I

Rhinolophus canuti canuti Thomas and Wroughton, 1909

Java

Formerly thought conspecific with *creaghi* by Hill (1958)

Rhinolophus canuti timorensis Goodwin, 1979

Timor I

Rhinolophus coelophyllus Peters, 1867

Burma—N Malaya; Langkawi I

Placed in *arcuatus* group by Andersen (1905b) and by Tate and Archbold (1939) but removed, with *shameli*, to *philippinensis* group by Tate (1943); however, it has a very short palate.

Rhinolophus shameli Tate, 1943

Burma—Campuchea

Rhinolophus inops Andersen, 1905a

Mindanao I, Philippine Is

Rhinolophus rufus Eydoux and Gervais, 1836

Luzon I, Mindanao I, Philippine Is

Rhinolophus subrufus subrufus Andersen, 1905a

Luzon I, Mindoro I, Negros I, Philippine Is

Rhinolophus subrufus bunker Taylor, 1934
Mindanao I, Philippine Is

Rhinolophus arcuatus arcuatus Peters, 1871
Luzon I, Philippine Is

Rhinolophus arcuatus exiguus Andersen, 1905a
Mindanao I, Philippine Is

Rhinolophus arcuatus beccarii Andersen, 1907b
Sumatra

Rhinolophus arcuatus toxopeusi Hinton, 1925
Buru I, Molucca Is

Rhinolophus arcuatus angustifolius Sanborn, 1939
Wetter I, Southwest Is, Flores Sea

Rhinolophus arcuatus proconsulis Hill, 1959
Sarawak, Borneo

*Rhinolophus arcuatus mcintyre*i, subsp. nov.
New Guinea

*Rhinolophus arcuatus mcintyre*i, subsp. nov.

Holotype.—CM 63497. Adult ♀. 4 km ENE Telefomin, W Sepik Province, Papua New Guinea (05°06'S, 141°41'E). Obtained in limestone cave by hunter on 6 March 1980 and prepared by Duane A. Schlitter, field number 4598 and BBM-NG field series number 105904. Skin and skull.

Additional specimens (10).—PAPUA NEW GUINEA: W Sepik Province, 4 km ENE Telefomin, 10 (3 BBM-NG, 1 BMNH, 2 CM, 4 PNGM).

Diagnosis.—A large subspecies of *R. arcuatus*, similar in size to *R. a. proconsulis* but differing from this and from the other subspecies in more expanded internarial region; shorter, wider sella and larger, more inflated median anterior rostral swellings; differing further from *R. a. proconsulis* in smaller, less massive canine teeth; from *R. a. beccarii* in higher, less flattened anterior rostral swellings and from *R. a. angustifolius* and *R. a. toxopeusi* in relatively shorter tail; cranially a little larger than all except *R. a. arcuatus* and *R. a. proconsulis*.

Description.—Ears large, broad, anterior or medial margin slightly convex to pointed tip, posterior margin concavely emarginated just beneath tip, thereafter convex; well-developed rectangular antitragus; posterior part of pinna above antitragus with a series of transverse involutions; interior surface of pinna pilose at base of medial margin, lower third of outer or medial surface and external face of antitragus similarly haired; noseleaf large, almost covering muzzle, the anterior leaf supported anterolaterally by a well developed fleshy ridge; anterior leaf with slight median emargination prolonged poste-

riorly as a faint groove extending about halfway across the flange of the leaf (in contrast to *R. euryotis* in which broad ridges enclose laterally a median groove across the leaf, terminating posteriorly in a low median projection); surface of anterior leaf with a sparse cover of short, grayish hairs; each nostril with prominent, sub-tubular lappets; internarial region expanded into an angular, slightly cup-like structure, about one-third as wide as anterior leaf, not totally concealing nostrils; sella short, wide, at its base and for much of its length only slightly narrower than the internarial cup, tapering slightly in its upper part to rounded tip, its face with a moderate cover of short, grayish brown hairs; connecting process high, rounded, originating anteriorly at tip of sella; lancet densely pilose, with slightly concave margins rising to rounded tip, its upper part narrowed, almost spatulate; length of second phalanx of third digit more than one and one-half times the length of the first phalanx; fifth metacarpal very slightly longer than fourth (in contrast to *R. megaphyllus* in which the length of the second phalanx of the third digit is less than one and one-half times the length of the first phalanx and in which the fifth metacarpal is shorter than the fourth or equal to it in length); dorsal pelage mid-brown, the hairs creamy white at the base and for much of their length, with pale brown or brown tips; ventral surface paler, with much of the pale base color exposed.

Skull relatively large, with elongate, slightly inflated braincase and low sagittal crest; interorbital region abruptly narrowed; rostrum high, with slightly developed supraorbital crests, their junction enclosing a very shallow frontal depression; anterior rostral swellings large, wide, the median pair strongly inflated, high and projecting; palate short, its anterior edge on a line joining the centers of the posterior upper premolars (PM4-4), its posterior edge just in advance of a line joining the centers of the second molars (M2-2); basioccipital not especially narrowed; anterior upper premolar (PM2) small, in tooththrow, second lower premolar (pm3) very small, almost totally extruded.

Measurements.—See Tables 1 and 2.

Etymology.—This new subspecies is named after Thomas J. McIntyre in appreciation of his keen interest in Australasian mammals and enormous support and assistance in the junior author's research on Old World mammals.

Remarks.—In size *R. a. mcintyre*i tends towards the Philippine subspecies *R. a. arcuatus* and the Bornean *R. a. proconsulis*, differing in this respect from the geographically much nearer *R. a. angustifolius* from Wetter Island and *R. a. toxopeusi* from Buru in the Moluccas, or from *R. a. exiguus* from Mindanao in the Philippine Islands and *R. a. beccarii* from Sumatra. At present, however, all seem poorly represented in collections, and no proper assessment of geographic variation can be made.

Little mensural data are available for *Rhinolophus arcuatus*. Some mensural data were analyzed by using ANOVA of the UNIVAR program. The statistics generated are mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation. The program employs a single classification analyses of variance (F-test, significance level 0.05) to test for significant differences between or among means. Standard statistics and a comparison between samples of males and females from the type locality of *R. a. mcintyre*i are given in Tables 1 and 2. Although samples are small, results of the comparison indicate that males may be significantly larger than females for

Table 1.—Statistical comparison of selected external measurements of six adult male and five adult female *Rhinolophus arcuatus* mcintyreii from the type locality. Statistics given for each sex are mean, standard error, range, and coefficient of variation. Measurements for holotype (CM 63497) are listed in right column of table.

Measurements	Males			Females			
	Mean \pm 2 SE	(Range)	CV	Mean \pm 2 SE	(Range)	CV	Holotype
Total length	80.8 \pm 1.74	(78–83)	2.64	81.0 \pm 2.10	(77–83)	2.90	82
Tail length	18.5 \pm 0.68	(18–20)	4.52	17.8 \pm 1.17	(16–19)	7.32	21
Ear length	20.8 \pm 0.61	(20–22)	3.61	20.8 \pm 0.40	(20–21)	2.15	21
Weight	13.5 \pm 0.68	(13–15)	6.20	13.8 \pm 1.17	(12–15)	9.45	15
Length of tibia	23.0 \pm 0.53	(22.0–23.7)	2.80	23.1 \pm 0.69	(22.0–23.9)	3.33	23.9
Length of forearm	51.3 \pm 1.10	(49.8–53.4)	2.64	49.9 \pm 1.17	(48.6–51.7)	2.61	50.5
Length of third metacarpal	38.5 \pm 0.61	(37.6–39.5)	1.95	38.2 \pm 0.90	(36.6–39.1)	2.64	39.1
Length of third, first phalanx	14.5 \pm 0.45	(13.6–15.1)	3.83	14.3 \pm 0.35	(13.8–14.7)	2.73	14.7
Length of third, second phalanx	23.6 \pm 1.09	(21.7–25.7)	5.64	24.3 \pm 1.24	(22.9–26.4)	5.72	26.4
Length of fourth metacarpal	39.5 \pm 0.95	(38.0–41.5)	2.95	39.2 \pm 1.03	(38.1–41.0)	2.94	41.0
Length of fourth, first phalanx	9.8 \pm 0.42	(9.2–10.6)	5.21	9.6 \pm 0.35	(9.0–10.1)	4.14	9.7
Length of fourth, second phalanx	14.2 \pm 0.47	(13.5–15.0)	4.01	14.1 \pm 0.42	(13.5–14.7)	3.35	13.9
Length of fifth metacarpal	40.0 \pm 1.15	(37.7–41.4)	3.52	39.8 \pm 1.06	(38.6–41.7)	2.97	41.7
Length of fifth, first phalanx	11.2 \pm 0.28	(10.8–11.6)	3.04	11.1 \pm 0.38	(10.5–11.5)	3.87	11.3
Length of fifth, second phalanx	13.0 \pm 0.60	(12.2–14.1)	5.66	13.0 \pm 0.50	(12.2–13.7)	4.32	13.7
Width of anterior leaf	9.2 \pm 0.27	(8.7–9.7)	3.60	9.0 \pm 0.23	(8.7–9.4)	2.83	9.0
Width of internarial cup	3.3 \pm 0.07	(3.2–3.4)	2.50	3.3 \pm 0.12	(3.2–3.5)	4.02	3.5
Width of sella at base	2.4 \pm 0.04	(2.4–2.5)	2.12	2.6 \pm 0.16	(2.4–2.8)	7.10	2.7
Height of sella	2.9 \pm 0.08	(2.8–3.1)	3.37	2.8 \pm 0.10	(2.7–3.0)	4.01	2.7

Table 2.—Statistical comparison of selected cranial measurements of five adult male and four adult female *Rhinolophus arcuatus* mcintyreii from the type locality. Statistics given are same as in Table 1. Measurements for holotype (CM 63497) are listed in right column of table. Significant differences between samples are indicated by a single asterisk for $P \leq 0.05$ and double asterisks for $P \leq 0.01$.

Measurements	Males			Females		
	Mean \pm 2 SE	(Range)	CV	Mean \pm 2 SE	(Range)	CV
Greatest length of skull	23.0 \pm 0.20	(22.6–23.2)	0.95	22.2 \pm 0.31	(21.8–22.5)	1.39**
Condylolbasal length	20.3 \pm 0.24	(20.0–20.7)	1.30	19.6 \pm 0.17	(19.4–19.8)	0.87**
Condylolcanine length	19.1 \pm 0.17	(18.9–19.4)	1.02	18.6 \pm 0.12	(18.5–18.7)	0.62**
Width of rostral swellings	5.7 \pm 0.06	(5.6–5.8)	1.24	5.5 \pm 0.08	(5.4–5.6)	1.48**
Least interorbital width	2.0 \pm 0.17	(1.7–2.1)	9.95	2.0 \pm 0.12	(1.9–2.1)	5.77
Zygomatic breadth	10.4 \pm 0.11	(10.3–10.6)	1.18	10.2 \pm 0.17	(10.0–10.4)	1.67
Breadth of braincase	9.2 \pm 0.17	(9.0–9.3)	1.41	8.9 \pm 0.10	(8.8–9.0)	1.07**
Mastoid breadth	10.2 \pm 0.10	(10.0–10.3)	1.12	10.0 \pm 0.17	(9.8–10.2)	1.70
Alveolar breadth of canines	5.6 \pm 0.14	(5.4–5.8)	2.73	5.5 \pm 0.13	(5.4–5.7)	2.28
Crown breadth of third molars	7.9 \pm 0.12	(7.7–8.0)	1.69	8.0 \pm 0.13	(7.8–8.1)	1.62
Crown length of maxillary toothrow	8.4 \pm 0.05	(8.4–8.5)	0.65	8.2 \pm 0.06	(8.1–8.2)	0.71**
Length of complete mandible, from condyles	14.4 \pm 0.12	(14.2–14.5)	0.93	13.9 \pm 0.10	(13.8–14.0)	0.69**
Length of right ramus, from condyles	14.8 \pm 0.17	(14.6–15.0)	1.26	14.5 \pm 0.17	(14.3–14.6)	1.20*
Crown length of mandibular toothrow	8.8 \pm 0.13	(8.6–8.9)	1.61	8.5 \pm 0.13	(8.4–8.7)	1.48*
						8.5

nine of the 14 cranial measurements tested. Generally, males have a longer skull, broader braincase, longer maxillary tooththrow, more inflated nasal swellings, and larger, longer mandibles and mandibular tooththrow. There were no significant differences between the samples for the external measurements that were tested. Except for total length, tail length, and weight, sample variances were equal.

Individual variation, as expressed by coefficients of variation, were generally low for both external and cranial measurements. Of the cranial measurements, least interorbital width was the only measurement with a value greater than 3. For the external measurements, 24 of the possible 38 coefficients of variation were less than 4. Exclusive of weight, only two measurements for females, length of tail and width of sella at base, had CVs greater than 6. Because males of *R. a. mcintyre* seem larger than females in most cranial measurements, future taxonomic studies of this species should allow for such secondary sexual variation in cranial measurements.

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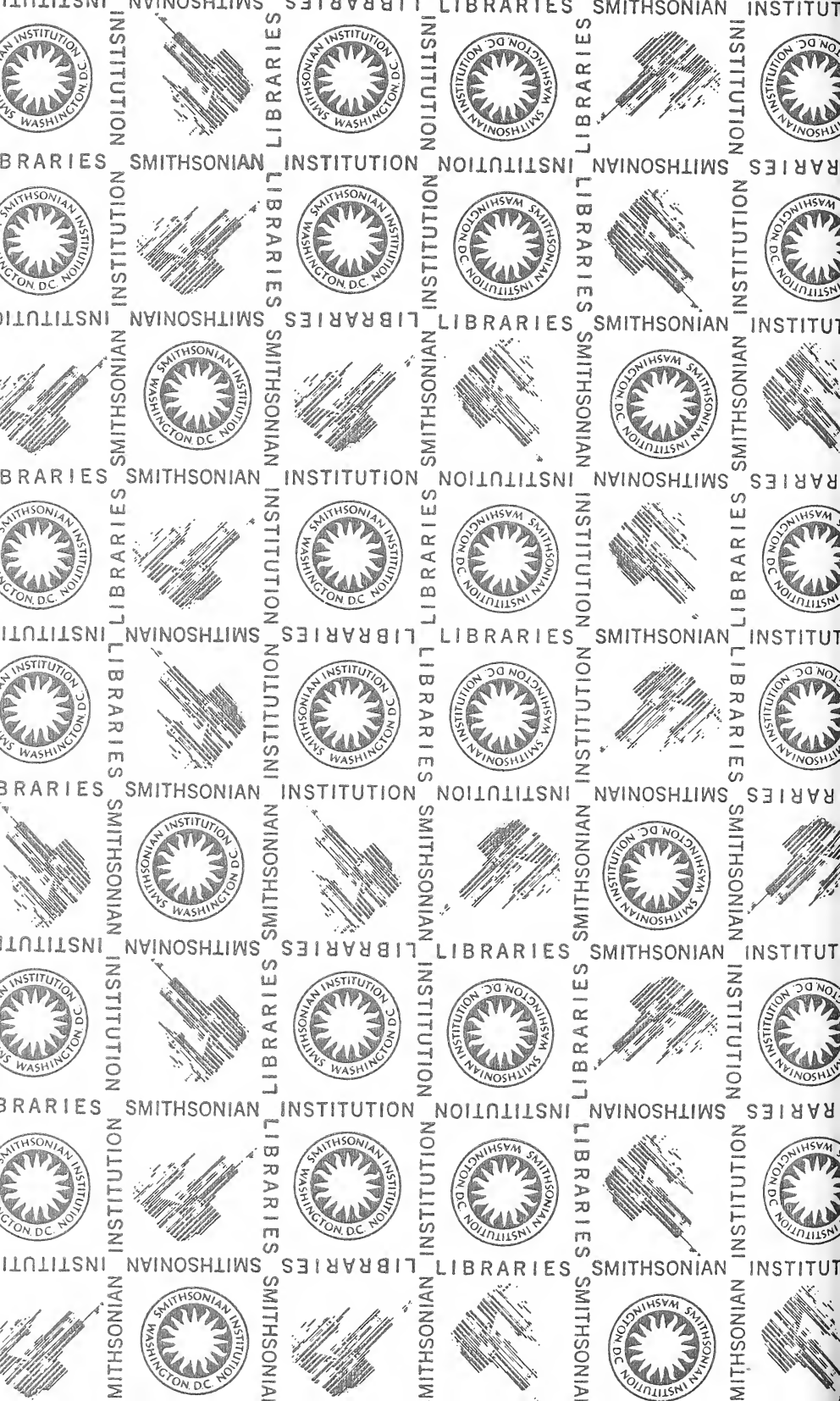
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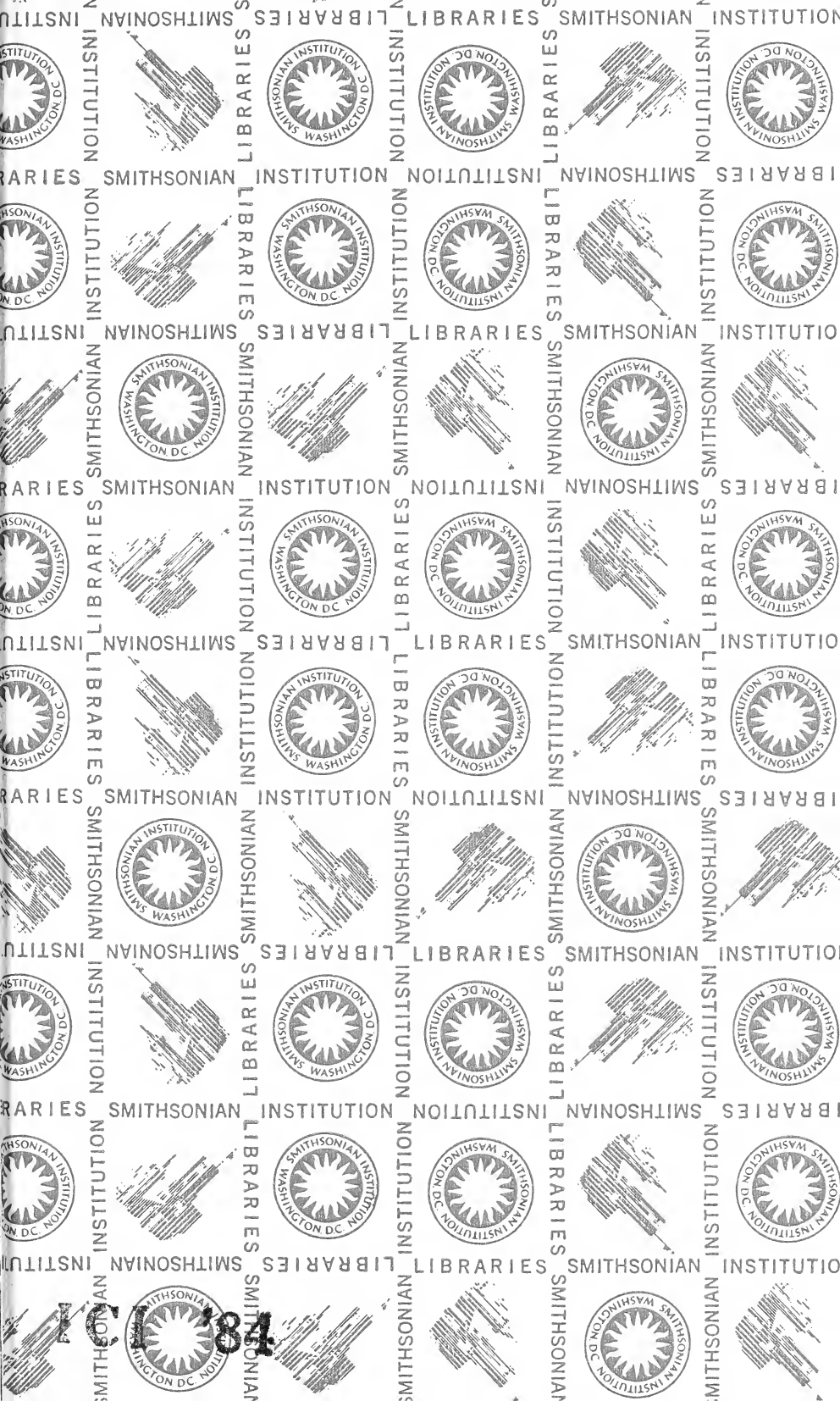
Specimens were divided among the mammal collections of the Bernice P. Bishop Museum—New Guinea collection (BBM-NG); Papua New Guinea National Museum and Art Gallery (PNGM); and Carnegie Museum of Natural History (CM). Additionally one CM specimen has been deposited in the British Museum (Natural History), London (BMNH).

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